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Individual differences and ageing effects in mental rotation

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Declaration

I hereby declare that this thesis is of my own composition, and that is contains not material previously submitted for the award of any other degree. The work presented in this thesis has been executed by myself, except where due acknowledgement is made in the text. All analyses reported in this thesis are original and were carried out by myself with a great amount of help from my supervisors Prof. Sergio Della Sala and Dr. Elena Gherri.

Signed,

30 Oct 2018

Binglei Zhao

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The four-year journey leading to the materialisation of this thesis would not have possible without the people around me.

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Note

Modified version of Experiment 1 has been published prior to the submission of this thesis. Experiment 2-7 are, at the time of writing, under review. For references, see the list of publications in Appendix C. In order to acknowledge the contributions of co-authors advisors, “we” will be used instead of “I” throughout this thesis.

All research reported in the following chapters of this thesis has been reviewed and approved by the University of Edinburgh’s Psychology Department Research Ethics Board. All analyses were conducted using the Brain Vision Analyser version 2.0.2 (Brain Products, Munich, Germany), Matlab R2016a (http://www.mathworks.com/products/matlab/) and IBM SPSS Statistics for Windows, version 22 (IBM Corp., 2010).

Abstract

There is a long-lasting debate as to whether mental imagery plays a functional role in cognition: one view states that mental imagery indeed plays a key functional role in cognitive processing, whereas other views suggest that propositional information is sufficient to complete a cognitive tasks and mental imagery is just an epiphenomenon. Recently, an alternative suggestion was proposed to reconcile these two hypotheses, namely that a range of strategies could be adopted to fulfil the demands of a given cognitive task.

This thesis was motivated by the general question: What specific strategy could be adopted in cognition in terms of individuals differing in their visual imagery vividness. To this end, mental rotation (MR) tasks were used to investigate individual performance in mental imagery, both in behavioural experiments and event-related potentials (ERPs) studies. Participants were classed according to their vividness of visual imagery (VVI) as individuals with lower and higher VVI. In behavioural experiments, lower and higher VVI individuals were assessed with MR tasks with different task demands. Whereas no group difference were observed in processing simple objects, differential performance was observed in processing more complex visual stimuli: lower VVI individuals were more likely to use piecemeal transformation, whereas higher VVI individuals were found could automatically simplify the task by transferring partial representation of the visual stimuli in their minds' eyes. In the following ERP studies using a standard letters rotation task, longer

MR execution time was observed in lower than higher VVI individuals. Rotation-related negativity (RRN) amplitudes were more pronounced in lower as relative to higher VVI individuals. In addition, the onset of RRN was found delayed in lower as compared to higher VVI individuals, while the onset of did not differentiate the two groups. These findings suggest that lower VVI individuals complete the MR process proper later than those with higher VVI. Higher VVI individuals are more able to generate simplified visual representations that can be easily rotated, whereas lower VVI individuals, who are more likely to create less accurate mental representations, might extract and represent additional information from the visual stimuli and therefore produce a longer MR execution time.

M.X., an individual who reported the sudden loss of his visual imagery ability was also recruited for an ERP experiment with a standard letter rotation tasks. He performed as well as his age, sex, IQ-matched controls. In addition, he showed the typical linear pattern in RTs as did in his controls did. But differential performance was detected in ERP data. In mirror letters, RRN was detected in the control but not in M.X. This finding suggests that the imagery task could be completed in the absence of the visual representation. Interestingly, in processing normal letters, RRN was observed in both M.X. and the control group, supporting the idea that non-depictive representation could be generated and adopted in MR processing. In turn, this result suggest that RRN is a general index for MR processing, regardless of the format of the mental representation, depictive or descriptive.

We then tested our hypothesis from another point of view by investigating whether one could adopt different strategies in MR tasks with different visual stimuli. Specifically, we explored which properties of the visual stimuli are more likely to predict the strategy selection in MR tasks. A behavioural MR experiment with polygon stimuli was conducted aiming at testing the two commonly used strategies used in MR tasks with different types of stimuli. Firstly, the segment number and the number of vertices in polygon stimuli were manipulated to test which property of the visual stimuli is more likely to influence the strategy selection in MR tasks. Secondly, the role of distractors was examined by comparing the stimulus complexity effect in both with- and without-distractors conditions. The results revealed that the number of segments affected the slope of the linear function relating response times to rotation angle but the number of vertices in the polygons did not. This suggests that a holistic strategy was more likely to be adopted in processing integrated objects, whereas a piecemeal transformation was at play in processing multi-part objects. In addition, the stimulus complexity effect was observed in the with-foil condition but not in the without-foil one, providing a direct evidence to support the role of distractors in MR tasks.

We then supplemented the investigation of the use of different strategies to comply with MR tasks by further examining if the largely document ageing effect in MR tasks could be explained by strategy selection. Younger and older participants were assessed with a series MR tasks with different task demands. Their visual

imagery vividness was controlled. In processing simple objects, the performance of the two age groups was comparable. However, systematic differences were observed between the mental rotation rates of younger and older adults while processing complex objects. Younger participants were faster in processing complex than simple objects, whereas older participants were slower in rotating complex than simple objects. These results revealed that different mental rotation strategies were selected by the two age groups. A simplified representation of the objects was generated and transformed by younger participants in their mind's eyes, while a piecemeal transformation strategy was adopted by older participants.

In the ensuing ERP study with simple MR tasks using characters, age-associated slowing was observed in both behavioural and ERPs measures. While the RRN was already present in the early time windows in younger adults (350-500ms), it only emerged in the late time window (500-650ms) in older participants. Consistent with this observation, the onset of the RRN was delayed in older as compared to younger participants. These results suggest that MR processes occur later in older adults and demonstrate that the initial phase before MR proper is one source of the age-related slowing observed in MR tasks. Possible accounts for this age-associated slowing are a prolonged phase of stimulus encoding and/or selective difficulties in directing attention away from the external stimulus towards its internal mental representation.

One more study was conducted to explore the general cognitive and neural mechanism underlying MR tasks. To better understand the normal-mirror difference in MR processing, we replicated Núñez-Peña and Aznar-Casanova's ERPs study (2009). The timing course of the planar rotation in normal letters, the planar and non-planar rotation in mirror letters were explored separately for each rotation angle. Moreover, we investigated the temporal relationship between these three processes for each angle. The result uncovered a complex cognitive process underlying MR process with mirror letters in which the non-planar rotation was found to occur at different time as relative to planar rotation for each rotation angle.

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Figure 5-4. Brain potential performances in mirror letter rotation. The left panel shows the mean ERP amplitudes elicited at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) by rotated (X°; dotted line) and upright letters (0°; solid line) in mirror letters separately for each rotated angle (30°, 60°, 90°, 120°, and 150°). The right panel presents the topographic mapping of the corresponding ERP difference between upright and rotated letters (planar rotation) for mirror letters in successive 50ms time windows from 300 to 1000ms post-stimulus separately for each rotated angle (30°, 60°, 90°, 120° and 150°). Intervals with significant effects of rotation angle within the intervals of rotation angle × stimulus type interactions for each

Chapter 1

Literature Review

1.1 Introduction

There is a long-standing debate on whether or not visual imagery plays a functional role in cognition (see review in Bartolomeo, 2008). One view suggests that propositional information is sufficient to complete an imagery task and mental imagery is just an epiphenomenon (Pylyshyn, 1981, 2003). Others maintain that imagery plays an essential functional role (e.g. Kosslyn, Thompson & Ganis, 2006; Paivio, 1971). This debate is intertwined with the nature of visual imagery (see review in Kosslyn, Ganis & Thompson, 2001; Pearson, Naselaris, Holmes & Kosslyn, 2015) as to whether the internal representation is "depictive" (picture-like; Kossly & Thompson, 2003; Slotnick, Thompson & Kosslyn, 2005) or "descriptive" (symbolic, language-like; Marmor & Zaback, 1976; Pylyshyn, 2002).

Recently, Pearson and Kosslyn (2015) argued that the internal image could be presented with multiple formats. The multiple formats of representations may vary with the different categories of the visual stimuli and could also be accounted by individual difference (Pearson & Kosslyn, 2015; Reeder, 2017). For example, the early visual cortex, a low level visual structure, was suggested plays a functional role in processing simple stimuli (Thirion et al., 2006), while less contribution was detected in imagery of complex objects (Lee, Kravitz & Baker, 2012). Moreover, the activation of the early visual cortex was reliably correlated with individuals' subjective rating on their visual imagery vividness (Cui, Jeter, Yang, Montague & Eagleman, 2007; Lee, Kravitz & Baker, 2012; Olivetti Belardinelli et al., 2009). That is to say, individual difference shapes the content of the visual representation (Bergmann et al., 2016; Pearson, Rademaker & Tong, 2011; Reeder, 2017).

As Pearson and Kosslyn suggested (2015), all the multiple formats of representations could be used in mental imagery tasks. Depending on the different format of representation, a range of strategies may be available to be adopted in cognition task. This approach would reconcile the two campuses of the debate on whether imagery does play a functional role or not (Geiser, Lehmann & Eid, 2006; Logie et al., 2011; Zeman et al., 2010). For example, one may rely on their depictive representation to perform the task, but others may use analytical strategy when they failed to generate a pictorial presentation but a symbolic one.

This thesis aimed to investigate this hypothesis on whether different strategies could be adopted in MR tasks. We adopted mental rotation (MR) to assess mental imagery ability and tested from two points of views: 1) whether individuals used different strategies in the same MR tasks and 2) whether different strategies adopted in processing different visual stimuli. As ageing effect on MR process have been largely documented, in this thesis we also looked at whether such ageing effect in MR could be accounted for by the different strategy selection in younger and older adults. In addition, normal-mirror difference in MR processing was also investigated to facilitate our understanding of the mechanism underlying normal and mirror rotation.

Behavioural and event-related potential (ERP) approaches were applied in this thesis. The behavioural MR paradigm was firstly introduced by Shepard and Metzler (1971) where participants were asked to compare a pair of arm-like cube objects rotated in three-dimensional (3D) space relative to one another and to determine whether they are the same objects in different rotation angles or mirrored ones. The MR experiment paradigms used in ERP studies in those by Cooper and Shepard (1973; see review in ERP studies in Heil, 2002) are different from the behavioural ones. ERP studies investigating the neural mechanism of MR have primarily used familiar stimuli (e.g. letters or digits). Typically, in these ERP studies a single letter is briefly presented on the screen in one of two possible versions (standard vs mirrored) and with different rotation angles. In order to perform the letter version judgment, participants are assumed to complete a "orientation–identicalization" process (Heil, 2002) in which

the stimulus representation is mentally rotated in a continuous way until it can be aligned and compared to its canonical representation stored in memory. Differential performances were determined between these two experimental paradigms with slower mental rotation rate (MR rate) observed in two-stimulus type than the single-stimulus paradigm (Shepard & Metzler, 1988).

In addition, differential performances were observed between object rotation and the rotation of human body parts (e.g. hands; Kosslyn, Digirolamd, Thompson & Alpert, 1998), suggesting distinctive mechanisms behind the object and body rotations. Therefore, in all the experiments reported in this thesis, object but not body rotation was used to test the different mental representation and strategy selection in MR tasks in terms of different types of stimuli, individual difference in visual imagery vividness as well as ageing.

In this introductory chapter, five relevant areas of study are reviewed: cognitive processes underlying MR processing; strategy selection in MR tasks; individual differences in strategy selection in MR; ageing effects in MR; and MR processing for identical and mirror images. These areas of study are fundamental to the points of interest investigated in all the empirical experiments reported in Chapters 3, 4 and 5.

1.2 Cognitive Process underlying MR Processing

As briefly introduced before, in a typical MR experiment, participants are asked to compare a pair of objects rotated in two-dimensional (2D) or three-

dimensional (3D) space relative to one another and to determine whether they are the same objects in different orientations or mirrored ones (Shepard & Metzler, 1971). Crucially, on each trial one of the objects is rotated between 0 and 180 degrees on different trials (Shepard & Metzler, 1971). Response times (RTs) increase linearly with rotation angle in both identical and mirror conditions (Shepard & Metzler, 1971; Cooper & Shepard, 1978). A consistent number of behavioural experiments confirmed this linear pattern of RTs in MR tasks with both familiar (e.g. alphanumerical characters, hands, or faces) and unfamiliar stimuli (e.g., polygons or arm-like cube objects). These findings have been interpreted as evidence for a dynamic imagery process based on a visual representation of the object akin to the actual physical rotation of the object (Shepard & Metzler, 1971; Shepard & Cooper, 1982).

According to the traditional theories of MR, at least five cognitive sub-phases can be envisaged in MR processing (Cooper & Shepard, 1973; Corballis, 1988; Shepard & Cooper, 1982): (a) perceptual encoding of the presented objects; (b) identification/ discrimination of the object and its orientation; (c) the pure MR processing; (d) judgment of parity; and (e) response selection and execution. Empirical evidence suggests either that these sub-processes are organized in a strictly sequential manner (Stoffels, 1996) or that consecutive processes do overlap but only to a very small extent (Heil, 2002; Ruthruff & Miller, 1995; see Figure 1-1 for example).

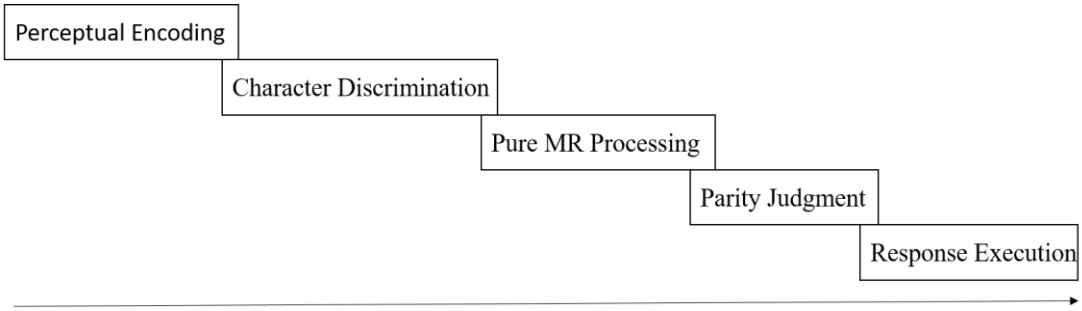

Figure 1-1. Partial overlap model of cognitive process underlying MR tasks.

Accordingly, the two elements (slope and intercept) forming the linear equation describing the pattern of RTs measured in a MR task $y = \alpha x + \beta$ (where y represents RTs and x represents the rotation angle) have their corresponding meanings in different cognitive sub-processes of MR. The slope of RTs function (α) was assumed to reflect how fast the internal representation was being rotated in one's mind (MR rate in the pure MR process) and the intercept (β), the cut off in y-axis, was assumed to reflect the processing time required in the other cognitive sub-processes including (a) perceptual encoding of the presented objects; (b) identification/ discrimination of the object and its orientation; (d) judgment of parity; and (e) response selection and execution (Cooper & Shepard, 1973; Just & Carpenter, 1976, 1985).

As the initial and a key sub-process in MR tasks (Paschke, Jordan, Wüstenberg, & Baudewig, 2012), the performance of visual perception (sub-process (a)) was found to affect the onset of its sequentially following process of MR (Heil & Rolk, 2002). According to the continuous flow models (e.g. Eriksen & Schultz, 1979; McClelland, 1979) and the model of Shepard and Cooper (1982), the perceptual information extracted from the visual stimuli needs to be transmitted continuously to the next stage

(Marr & Nishihara, 1978; Marr, 1982; Pinker, 1984). Heil and Rolk (2002) manipulated the perceptual quality of the visual stimuli (Experiment 1 in Heil & Rolk, 2002) by presenting either black letters on a white background without any noise, or by presenting black letters on a grey background with visual noise added. The onset of rotation-related negativity (RRN), indicating the pure process of MR, was found to be delayed in time when the quality of the stimuli was reduced, providing direct evidence for the sequential manner between visual perception and the pure MR processing.

It is suggested that object discrimination participates in MR processing (Corballis, 1988). According to Corballis's speculation (1988), there are at least two levels of object discrimination in MR tasks: one happens prior to MR processing to discriminate rotated objects (refer to sub-process (b)), whereas the second is a parity judgment after MR processing (refer to sub-process (d) which will be discussed later in this chapter). For the first basic object discrimination, it is known that to discriminate a rotated letter-like symbol, or to discriminate a rotated character as a digit or a letter could be simply executed in the absence of MR processing. This is indicated by the independent RTs of rotation angles (Corballis & Nagourney, 1978; Eley, 1982) and no activation of the frontal-parietal cortex, the area implicated in MR (Weiss et al., 2009). However, such basic-level object discrimination, in turn, was suggested as needed for completing identical-mirror parity tasks and typically before the execution of MR processing. MR processing refers to the process by which internal

representation is rotated in one's mind until it appears familiar enough to be recognized. Therefore, it is logically difficult to understand how one could execute this process without knowing the canonical view of the stimuli as pointed out by Corballis (1988).

The participation of such basic-level object discrimination in MR tasks was later verified and it was found that this sub-process occurs before the onset of MR processing (Heil & Rolk, 2002; Milivojevic, Hamm, & Corballis, 2011; Ruthruff & Miller, 1995). By using an additivity/ underadditivity diagnostic, Ruthruff and Miller (1995) tested the temporal relationship between stimuli discrimination and the pure MR process. The object discrimination difficulty was manipulated by means of the similarity between two character letters (e.g., dissimilar between y and r and similar between y and g in Experiment 1 in Ruthruff & Miller, 1995), or by means of the similarity between the character letter and its distorted versions (Experiment 2 in Ruthruff & Miller, 1995), or pairing within a block either two characters that, in the fonts used, were approximate mirror images of one another (e.g. F and 7) or two visual dissimilar characters (F and g). Underadditivity between stimulus discrimination and rotation effect was consistently found in all three experiments, supporting the model that stimulus discrimination and MR processing are partially temporally overlapped. Heil and Rolke (2002) replicated Ruthruff and Miller's experiment (1995) in their ERP study (Experiment 2) and found that the onset of MR processing was delayed in time by experimental manipulations with prolonged character discrimination. All these findings provided evidence that MR processing happened sequentially after, or with

partial temporal overlap, with the object discrimination according to the model of Shepard and Cooper (1982).

Discrimination of the rotation angle was also suggested as preceding the pure process of MR (Corballis, 1988). However, few studies investigated whether rotation angle affects the stimuli discrimination process in MR tasks and whether this sub-process precedes the pure process of MR. The rotation angle effect on discrimination of rotated objects was suggested to be dependent on the level of identity (Hamm & McMullen, 1998). The rotation angle can affect the subordinate-level (e.g., between objects within a semantic category), but not the superordinate-level (e.g. between-category) or basic-level categorisation (Hamm & McMullen, 1998). However, it is worth noting that these suggestions are all based and reasoned from behavioural measures, RTs or the accuracy of response, which reflect the combined contribution of multiple, interacting stages of neural processing so that the rotation angle effect on the pre-processing phase in MR may not translate into increases in RTs or impaired accuracy especially in the temporal partial overlap model (Ruthruff & Miller, 1995). Recently, Milivojevic and her colleagues (2011) used ERPs to address this issue. They found a rotation angle main effect on the ERPs amplitudes between 160 and 220ms, a neural marker of object classification occurring temporally before the MR processing. These findings provided direct evidence that the rotation angle of the stimuli could be discriminated before the internal representation being rotated in one's mind.

In addition, there are two other sub-processes – parity judgment (sub-process (d)) and response execution (sub-process (e)) – which, it has been suggested, are MR tasks which occur after the completion of the pure MR process or with a temporal overlap with MR processing. Cooper and Shepard suggested that participants already prepared to make a 'normal' response at the beginning of each trial (1975). If this were the case, participants could judge the parity of the stimuli and execute their response before the MR processing was completed; if a mirror response is required, the pre-prepared execution will be inhibited but the non-prepared response made. This temporal relationship between response preparation and MR processing has been tested (Heil, Rauch, & Hennighausen, 1998). In a MR task, Heil et al. (1998) analysed the lateralized readiness potentials (LRPs), an index to determine the appearance of response preparation (Deecke, Grozinger, & Kornbuber, 1976) in both the presence and the absence of an overt response (e.g. Miller & Hackley, 1992). In the no-go trials where the stimuli were presented in their mirror versions, LRPs were reliably obtained, providing evidence for the idea that the response preparation occurred before MR processing was finished. In addition, it was suggested that motor simulation and execution also participated in MR tasks as revealed by the activation of the motor regions in the precentral cortex in dozens of neuroimaging studies (see review in Zacks, 2008). This functional role was proved by a study of Parkinson's disease (PD) (Lee, Harris & Calvert, 1997). The patients with motor deficits were found to be impaired in MR tasks as compared to their control group (Lee et al., 1997). Specifically, in a

single-trial functional magnetic resonance imaging (fMRI) study, right motor cortex was suggested to be associated with the button press at the end of the task period (Richter et al., 2000).

1.3 Strategy Selection in MR Tasks

Two commonly used MR strategies have been identified: holistic and piecemeal. The holistic strategy relies on depictive representations which are rotated as a whole in one's mind's eye akin to the actual physical rotation (Cooper & Shepard, 1984; Metzler & Shepard, 1974). For example, as depicted in Figure 1-2, the object on the left panel could be encoded and rotated as a whole.

On the other hand, piecemeal transformation refers to the discrete manipulations of symbols/propositions rotated piece-by-piece (Pylyshyn, 1973, 1981). The content of the rotated representation varies. One could transform a partial image of the visual stimuli in congruence with the comparison object and then apply the same rotation to the other parts of the object to see if they match (Khooshabeh, Hegarty & Shipley, 2013). For example, as depicted in Figure 1-2, an individual triangle in the visual stimulus on the left was transformed one piece at a time to make the comparison with the one on the right. Alternatively, spatial features could be transformed several times to make comparisons. As shown in Figure 1-2, for example, the relative location of each of the two triangles on the right of the object could be rotated one-by-one to compare with the object on the right.

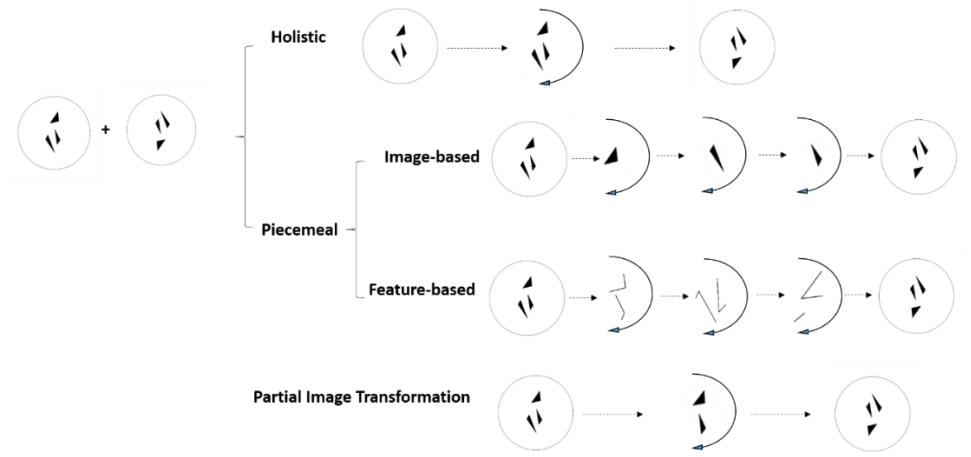

Figure 1-2. Examples of the cognitive processes underlying the possible strategies adopted in MR tasks.

In addition, partial image transformation was suggested as a third possible strategy, in which a partial image of the visual stimulus could be encoded and rotated in one's mind to complete the MR task (e.g., Cooper & Podgorny, 1976; Folk & Luce, 1987; Liesefeld & Zimmer, 2013; Xu & Franconeri, 2015). The difference between partial image transformation and a holistic strategy is the content of the internal representation. As shown in Figure 1-2, a partial image of the visual stimuli is encoded in partial image transformation but not the whole image as performed in holistic processing. Liesefeld and Zimmer's experiment (2013) found that only rotation-relative information is rotated. In their study (Liesefeld & Zimmer, 2013), participants were assessed with three types of stimuli, simple, visually complex (with additional rotation-independent information) and complex (with additional rotation-dependent information) stimuli. It was found that the visually complex objects could be rotated as efficiently as the simple ones, whereas a much slower MR rate was observed in

processing the complex stimuli. More recently, Xu and Franconeri (2015) tested the ability to rotate multi-part objects and found participants could maximally encode two pieces and rotate this partial image of the stimulus and not the whole object as indicated by a holistic strategy.

Several means could be used to detect the possible strategy selection including behavioural (the estimated slope in RTs) (Cooper, 1975; Cooper & Podgorny, 1976), electrophysiological, neuroimaging (Hugdahl, Thomsen & Ersland, 2006) and eye-tracking measures (Nazareth, Killick, Dick & Pruden, in press; Scheer, Mattioni & Jansen, in press). The following sections summarize the behavioural and electrophysiological measures for the pure MR process, the two measures used in my PhD experiments, and explain how they could be used to detect the strategy selection in MR tasks.

1.3.1 Behavioural measures for MR

By using either strategy, the response times (RTs) in MR tasks linearly increase with the increase of the rotation angle (Cooper & Shepard, 1984; Kosslyn, 1981; Pylyshyn, 1981; 2003; Shepard & Metzler, 1971).

The stimulus complexity effect on the estimated slope was suggested and used as an indicator for these two possible strategies, holistic and piecemeal transformation (Cooper, 1975; Heil & Jansen-Osmann, 2008; Kail, Carter & Pellegrino, 1979; Khooshabeh et al., 2013). By comparing the theoretical accounts for these two strategies, Cooper (1975; see also Cooper & Podgorny, 1976) postulated that the slope

is only dependent on the rotation angle if holistic strategy was at play, whereas in piecemeal transformation the slope was dependent not only on the rotation angle, but also the stimulus complexity. As shown in Figure 1-3, in piecemeal transformation, as the complexity of the internal representation increases, more time is needed to replace the features/nodes and the spatial networks among these features/nodes during MR processing in piecemeal transformation and therefore, a steeper slope would show in RTs function of rotation angles. However, in holistic processing the internal representation is maintained and manipulated as a whole regardless of its complexity. In this context, piecemeal could be distinguished from holistic by predicting an increment of MR rate with the increasing stimulus complexity.

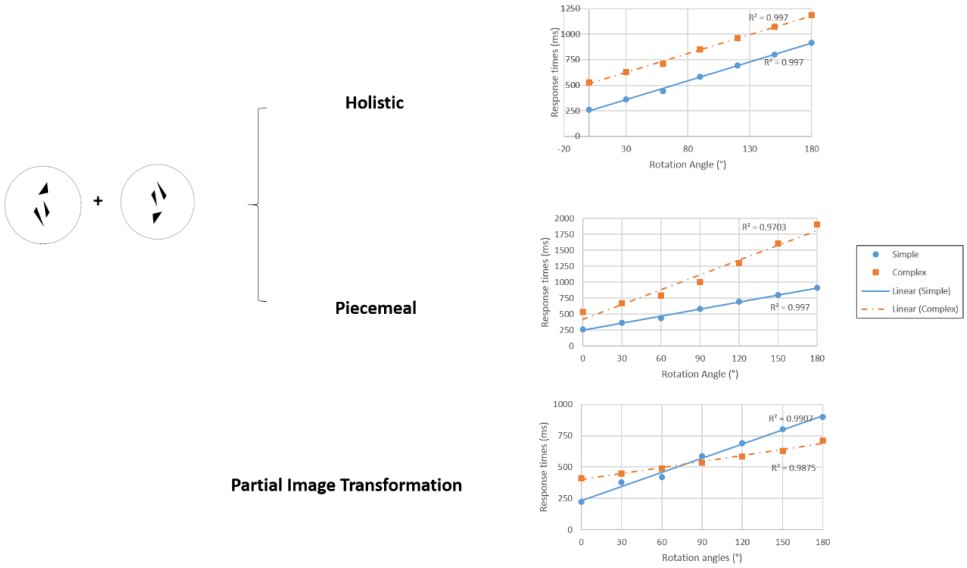

Figure 1-3. Examples of RTs function of rotation angles when holistic, piecemeal transformation and partial image transformation was adopted in MR tasks respectively.

On the other hand, a shallower slope in RTs function was assumed to reflect the utilization of partial image transformation. Seven additional cubes were added in Shepard and Metzler's typical arm-like cube objects (1971) to raise the complexity level of stimulus in Yuille and Steiger's study (1982; Experiment 2). A shallower slope was observed in processing more complex stimuli than that in the standard simpler objects (as show in bottom panel in Figure 1-3 as an example). According to the authors' interpretation, this finding suggested that participants performed faster in more complex stimuli than simpler ones because they have the ability to automatically simplify the task by detecting the redundant information and maintain a partial image of the stimuli for MR processing.

Particularly, the non-linear pattern was also observed in RTs function of rotation angle in accordance with the alternative analytical strategy which did not rely on the internal representation. For example, a patient showed this non-linear pattern in his RTs performance (Zeman et al., 2010). According to his debrief, he could not rotate the image in his mind's eye, instead he compared the individual cubes in Shepard and Metzler's typical arm-like cube objects (Zeman et al., 2010).

1.3.2 Electrophysiological measures for MR processing

Electrophysiological measures have also been used to characterise the pure process of MR. Empirical evidence strongly suggests that the amplitude modulation as a function of the rotation angle of the character (or called rotation-related negativity: RRN) is functionally and temporally related to the pure process of MR (Rösler, Heil,

Bajric, Pauls & Hennighausen, 1995; for a review see Heil, 2002). Peronnet and Farah (1989), Rösler et al. (1990), and Wijers et al. (1989) first reported that in a parity judgment task, the ERPs recorded over the parietal scalp revealed a pronounced positive component, a P300; the amplitude of this positive component became relatively more negative (or less positive, respectively) with an increasing rotation angle of the characters presented.

The speculative interpretation of the functional relationship between RRN and the pure MR processing was substantiated in recent years. Heil and his colleagues (1996) provided the first evidence that MR acts as a necessary requirement for RRN. In their study (Heil, Bajric, Rösler & Hennighausen, 1996), ERPs were recorded during the presentation of rotated characters under two different instructions: parity judgment and character classification. As shown in Figure 1-4, top panel, the ERPs amplitude modulation due to the rotation angle of the characters was obtained in the parity judgment task where MR is required, whereas RRN was absent in the character classification task where MR is not necessarily required (Corballis & Nagourney, 1978).

Moreover, MR processing was found sufficient to evoke RRN whereas the execution of giving a response is not necessary (Heil, Rauch & Hennighausen, 1998). Participants were instructed to give a response when a rotated normal character was presented on the screen but not respond if the character was presented in its mirrored version (Heil et al., 1998). MR processing is required in both normal and mirror

rotation before determining the parity (Koriat & Norma, 1985; Shepard and Metzler, 1971) and RRN was obtained both with and without the response condition, with no difference between them (Heil et al., 1998).

Furthermore, both stimulus difficulty level and the rotation angle were found to modulate the amplitude of P300 (Bajric, Rösler, Heil & Hennighausen, 1999). To figure out whether RRN is merely related to MR or also relative to the task difficulty, Bajric et al. (1999) further conducted another experiment where a cue presented 3,000ms before the character. The cue provided valid information about the rotation angle from the upright angle of the character. Therefore, the task difficulty was given by the cue and MR could not start until the character presented. The results revealed the opposite ERPs pattern in terms of task difficulty and MR processing: P300 elicited by the cue became more positive with the more difficulty of the task anticipated, whereas P300 elicited by MR became more negative with the larger rotation angle of the character.

The temporal relationship between RRN and MR processing was also substantiated (Heil & Rolke, 2002). As perceptual encoding of the presented objects and identification of the object are two sub-processes suggested to occur before the pure MR processing (Ruthruff &Miller, 1995), the perceptual quality of the character (Experiment 1) and the difficulty of character discrimination (Experiment 2) were manipulated to test this temporal model of RRN (Heil & Rolk, 2002). As shown in the bottom panel in Figure 1-4, RRN was observed as being delayed when either the

perceptual quality of the stimulus was reduced or when character discrimination was more difficult.

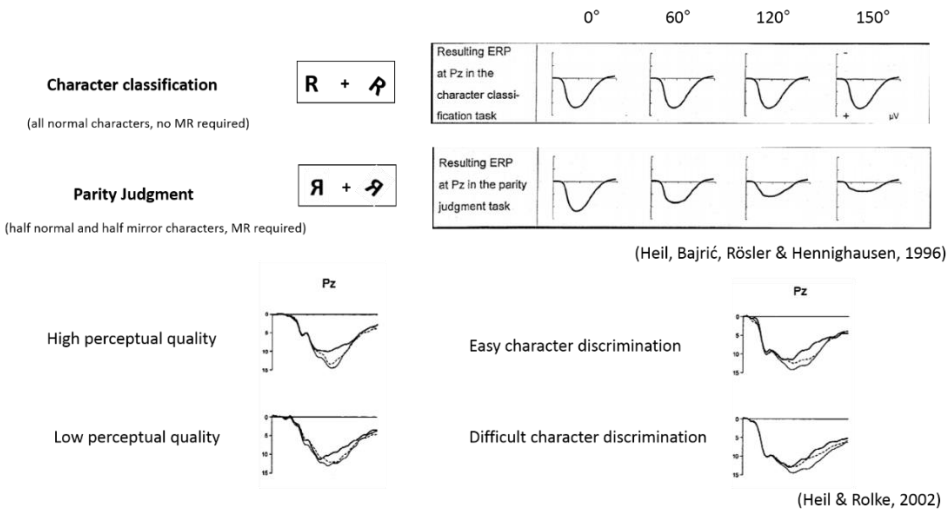

Figure 1-4. Examples of ERPs findings in each experimental condition to demonstrate the functional and temporal model of RRN and MR processing. The top panel presents the ERPs in character classification and parity judgment tasks respectively: RRN was evident in the parity judgment task but absent in the task of character classification (Heil, Bajrić, Rösler & Hennighausen, 1996). The bottom panels present the temporal model of RRN and MR processing in which the delayed RRN was observed when the perceptual quality of the characters was reduced or when the character discrimination was difficult (Heil & Rolke, 2002).

In summary, the onset of RRN could be used as a chronopsychophysiological marker for the onset of the cognitive process of MR. In addition, RRN could be used to detect the existence of the pure MR process. For example, if one used an alternative strategy to complete the MR task instead of MR processing, the amplitude modulation

of rotation angle, the RRN would not emerge as indicated in Heil et al.'s (1996) character classification task (see Figure 1-4, the top panel for example).

1.4 Individual Difference in Strategy Selection in Mental Rotation

Differential performance was detected in processing MR tasks across individuals in terms of age, spatial ability and visual imagery ability. For example, it is commonly found that men outperform women in MR tasks (Voyer & Hou, 2006; Titze, Heil & Jansen, 2010). In addition, men were observed to mentally rotate objects faster than do women (e.g., Astur, Tropp, Sava, Constable, & Marcus, 2004; Parsons et al., 2004; Peters et al., 1995). Many reasons have been proposed to explain this gender difference in MR tasks (Voyer, Voyer & Bryden, 1995; Jansen-Osmann & Heil, 2007b), for example "psycho-social" variation including stereotype threat, sex role identification, differential socialization (Flaherty, 2005; Terlecki & Newcombe, 2005), or the "biological-neural" accounts including genetic dissimilarities or hormonal differences (Dabbs, Chang, Strong & Milun, 1998; Davison & Susman, 2001; Grimshaw, Sitareios & Finegan, 1995; Schöning et al., 2007).

Recently, another possibility was raised to account for this individual difference in MR rate in terms of the strategy selection in MR tasks (Boone & Hegarty, 2017). Men were commonly found to rely more on a holistic strategy (Cochran & Wheatley, 1989; Geiser, Lehmann & Eid, 2006; Heil & Jansen-Osmann, 2008; Hugdahl, Thomsen & Ersland, 2006; Raabe, Höger & Delius, 2006), whereas women

were more likely to use an analytical strategy (Geiser, Lehmann & Eid, 2006; Heil & Jansen-Osmann, 2008; Raabe, Höger & Delius, 2006). According to Cooper's hypothesis (1975), analytical strategy requires more time to process more complex objects as compared to holistic strategy. Therefore, the different strategy selection across gender may account for the faster MR rate in men compared to that in women.

As spatial ability and visual imagery vividness are two related factors investigated in my PhD studies, the following sections will focus on how spatial ability and visual imagery vividness levels affect the MR performances respectively, especially in terms of the strategy selection.

1.4.1 Differential MR performances across individuals with different spatial abilities

Individual difference in MR performance has been reported for decades in terms of spatial ability (Egan, 1978; Lansman, 1981; Mumaw, Pellegrino, Kail & Carter, 1984; Pellegrino & Mumaw, 1980). It is notable that this individual difference in MR varies with stimuli familiarity and complexity as well as dimensionality.

First, differential performance across individuals with different spatial abilities could be detected on the intercept with more reliability in unfamiliar stimuli. The representation of an unfamiliar object, it was assumed, needed to be generated based on the external visual stimuli, whereas the process of familiar objects was assumed to rely more on a long-term memory representation (Stoffels, 1996). The distinctive mechanisms behind familiar and unfamiliar object processing, it was suggested, could

be accounted for by the presence of individual difference in unfamiliar but not familiar objects (Mumaw et al., 1984). In processing familiar stimuli (e.g. letters or digits), no differential performance on the intercept measurement was obtained between two groups of individuals differing in their accuracy in MR performances (Beste, Heil & Konrad, 2010; Mumaw et al., 1984). This result may indicate that the low-performance in MR tasks, at least for those participants recruited in Beste et al.'s (2010) and Mumaw et al.'s (1984) experiments, may not be due to the deficit in retrieving the representation from the long-term memory. On the other hand, in processing unfamiliar stimuli, a larger intercept was observed in low-spatial than high-spatial individuals in processing unfamiliar objects and this was interpreted as suggesting that low-spatial individuals require a longer processing time in encoding the visual stimuli as compared to high-spatial individuals (Egan, 1978; Mumaw, Pellegrino, Kail & Carter, 1984). However, it is notable that these stimuli were all 2D objects. When participants were assessed with unfamiliar 3D objects such as Shepard and Metzler's arm-like cube stimuli (1971), no significant difference in the intercept measure was observed between low- and high-spatial individuals (Khooshabeh et al., 2012).

In addition, group difference was also observed in the MR rate between low- and high-spatial individuals and has been explained by the different strategy selections. In processing 2D stimuli, high-spatial individuals were found to have performed faster than low-spatial ones, as indicated by the estimated slope in RTs function of rotation angle (Mumaw et al., 1984). Mumaw et al. (1984) speculated that high-spatial

individuals are able to generate more accurate internal representation and maintain such representation while rotating the object as a whole, whereas low-spatial individuals may fail to keep the complete the representation intact while rotating it and had to rotate the parts individually. This speculation is to some extent verified in a recent study (Göksun, Goldin-Measow, Newcombe & Shipley, 2013) by investigating the usage of gesture in a MR task. High- and low-spatial individuals were found to differ in the types of gestures used to convey static information: high-spatial individuals were more likely than low-spatial individuals to use gestures that captured the internal structure of the block forms. This is in accordance with Mumaw et al.'s view (1984) that high-spatial individuals are more likely to form robust and accurate information of the visual stimuli while rotating as compared to low-spatial individuals.

Bethell-Fox and Shepard (1988) conducted a training experiment and found that the strategy selection may be influenced by the stimulus familiarity. Participants were assessed with MR tasks before and after the training. A significantly faster MR rate was observed in the test after the training as compared to that in the pre-training test, suggesting that piecemeal transformation is more likely to be adopted in processing unfamiliar objects, whereas a holistic strategy could be at play when the stimuli is well-learned. Moreover, individual differences in strategy selection could also be detected. No individual differences were found for novel objects. However, in the after-training test, a longer RT was detected in two participants who reported having used a verbal/analytical strategy than that in those who reported using a holistic

strategy. According to the participants' debriefing, high-spatial ability individuals swapped their strategy to holistic when the stimuli were well-learned after sufficient practice and their RTs dropped rapidly. On the other hand, low spatial-ability individuals reported being unable to disengage from piecemeal transformation, and their RTs remained virtually the same before and after practice.

Due to the small sample, the estimated slope of RTs function the suggested indicator for strategy selection in MR tasks (Cooper, 1975; Cooper & Podgorny, 1976) – could not be used to analyse the individual differences in Mumaw et al.'s experiment (1984). However, this individual difference was obtained in a more recent ERP study (Beste, Heil & Konrad, 2010). In their study (Beste et al., 2010), participants were assessed with character letters while electroencephalogram (EEG) was used to record. Larger amplitude was detected in low-spatial individuals whereas smaller amplitude but larger involvement of parietal networks was recorded for high-spatial individuals. This result was interpreted in line with the idea of neural efficiency, postulating that high performances are associated with more efficient brain function (e.g. Haier et al., 1988). More specifically, high-spatial individuals may adopt a more efficient neural strategy by recruiting a larger neural network at a lower level of activation and perform better than low-spatial individuals.

The individual difference in strategy selection was also reported as varying with the stimulus complexity. Khooshabeh et al. (2013) used integrated and fragmented objects (see Figure 1-5, left panel) to assess high- and low-spatial ability

individuals. High-spatial ability individuals adapted to the task demand, using a holistic strategy in processing integrated objects but applying piecemeal transformation when mentally rotating fragmented objects, thus showing a steeper slope in fragmented stimuli than integrated ones (see Figure 1-5, right top panel). Low-spatial ability individuals showed similar performances in fragmented and integrated blocks (see Figure 1-5, right bottom panel), suggesting that they used piecemeal transformation for both fragmented and integrated objects.

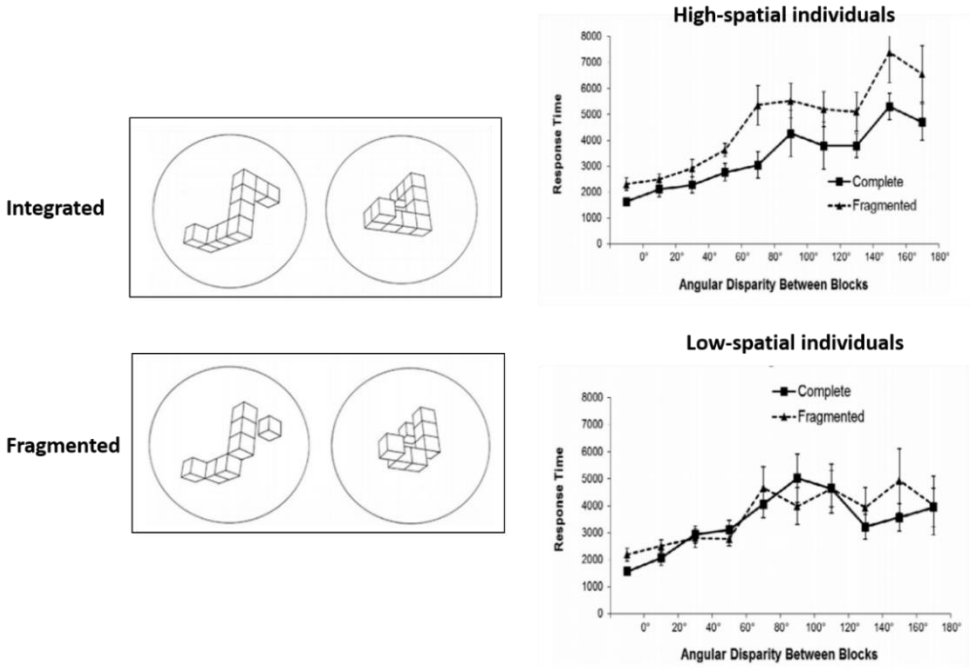

Figure 1-5. Visual stimuli used and participants' performance in Khooshabeh et al.'s experiment (2013). The left panel depicts the integrated and fragmented stimuli used in the stimuli. The right panel depicted the performance of high-spatial (top) and low-spatial individuals (bottom) in processing integrated (solid line) and fragmented objects (dotted line).

1.4.2 Differential performances across individuals with different visual imagery vividness

1.4.2.1 Definition of visual imagery vividness

Imagery vividness is often defined only intuitively as if participants and experimenter assigned the same meaning to terms based on primitive dimensions that are comprehensible but not wholly definable (Cornoldi et al., 1991). According to Mark (1972), vividness is "a combination of clarity and liveliness. The more vivid an image, therefore, the closer it approximates an actual percept" (p.83). McKelvie (1995) further provided a diagram of the quasi-perceptual characteristics of visual imagery vividness (see Figure 1-6). The clarity is defined as "the brightness of its colours and the sharpness of the outline and details" and the liveliness is defined as "how dynamic, vigorous and alive the image is" (Marks, 1999, p.570).

Richardson (1994) challenged this definition that vividness does not only reflect how accurately the internal representation generated corresponds to the percept. Instead, he emphasized that vividness reflects the degree of involvement with the imaged content, the feeling of 'being there' Moreover, it provides a sense of reality so that the imager could experience the liveliness, strength and intensity of the external stimuli.

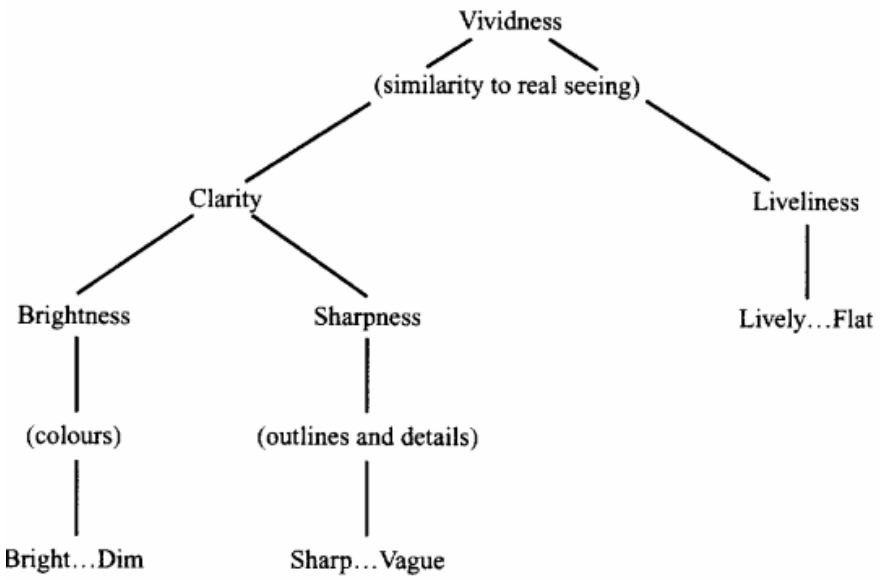

Figure 1-6. A summary of the vividness construct (McKelvie, 1995).

1.4.2.2 Measurements for visual imagery vividness

There are two commonly used questionnaires to subjectively rate imagery vividness. The Questionnaire upon Mental Imagery (QMI) was the first quantitative questionnaire of imagery ability focusing on the notion of vividness (Sheehan, 1967). There were 150 items in this questionnaire and participants have to imagine each item and rate their vividness of each imaged item along a 7-point scale (Sheehan, 1967). The Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973) was designed by expanding the visual scale of the QMI. There are four sets of items giving a total of 16 items in the VVIQ. Participants were instructed to imagine a scene, an activity or a person and rate the vividness of each image generated in their minds' eyes along a 5-

point scale. For example, participants were asked to imagine the scene of the front of a shop they often go to. This questionnaire was later revised and expanded to include 32 items (VVIQ-version2; VVIQ2) (Marks, 1995) so that the scale samples a wider range of imagery ratings, a reversal of its scoring of responses such that greatest vividness of imagery is now scored '5' rather than '1' and all rating are made only once with eyes closed. VVIQ2 has been used in a number of published studies (e.g. Logie, Pernet, Buonocore & Della Sala, 2011; Pearson, Rademaker & Tong, 2011) and with high reliability and validity to measure visual imagery use and experience (McAvinue, & Robertson, 2007; Campos, 2013)

1.4.2.3 The level of visual imagery vividness affects representation generation

As an essential and initial phase in MR, the different formats of visual representation can be explained to a large degree by individual's visual imagery vividness (Reeder, 2017; Olivetti Belardinelli et al., 2009). Binocular rivalry is a visual phenomenon when two different patterns are presented, one to each eye, one pattern reaches awareness while the other is suppressed. Pearson and his colleagues found (2008) the sustained imagery can bias the perception of an ambiguous display presented afterwards. In a following study (Pearson et al., see also Bergmann et al., 2016), the degree to which visual imagery primes perceptual dominance in binocular rivalry is found to be correlated with self-reported VVIQ2 score (Marks, 1995). For trials in which higher vividness was reported by the participants, a previously imaged item was more likely to emerge as dominant from the binocular rivalry representation

compared to the unimagined objects. These findings suggest that the level of VVI varies with individuals and significantly influences perception.

Neuroimaging studies also provided evidence for the positive correlation between the subjective reported visual imagery vividness and the format of generated internal representation, mainly indicated by the activation on the early visual cortex (V1) (see review in Reeder, 2017; Cui, Jeter, Yang, Montague, & Eagleman, 2007; Lee et al., 2012; Olivetti Belardinelli et al., 2009). Although it was found the contribution of V1 during mental imagery compared with extrastriate cortex (ESC) and object-selective cortex (including posterior fusiform sulcus, pFs and lateral occipital, LO) is much weaker than during perception of the same objects (Lee et al., 2012), it is not suggested that V1 does not play an essential role in visual imagery (Thirion et al., 2016). When visual imagery vividness was taken into account, Lee at al. (2012) found a reliable correlation between participants' subjective rating on VVIQ score (Marks, 1973) and the activation of early visual cortex (including V1 and ESC). This finding is in accordance with the finding in a previous fMRI study (Cui et al., 2007) whereby the early visual activity relative to the whole brain activity was found highly correlated with individuals' VVIQ rating (Marks, 1973). This correlation was also verified by using QMI, an alternative questionnaire assessing visual imagery vividness (Olivetti Belardinelli et al., 2009). In their study, participants were split into two groups, good- and poor imagers, based on the self-reported vividness of their visual imagery in an Italian version of QMI (Sacco & Reda, 1998, as cited in Olivetti

Belardinelli et al., 2009). Greater involvement of the early visual cortex was observed in higher compared to that in lower VVI individuals. This result was interpreted as supporting the hypothesis that individuals with higher VVI would create more analogical representations relying on the same specific neural substrates active during perception with respect to lower VVI individuals.

1.4.2.4 The level of visual imagery vividness affects strategy selection in MR

Recently, different strategies have been suggested to be adopted by individuals with different levels of visual imagery vividness (e.g. Logie et al., 2011; Zeman, Della Sala, Torrens, Gountouna, McGonigle, & Logie, 2010). As representation is a prerequisite for the upcoming MR processing (Marmor & Zaback, 1976), the different format of internal representation generated by individuals with different vividness levels of visual imagery may affect the strategy selection in MR tasks.

A good example of the possible use of strategies to address MR is the case of MX, a 65-year-old man who reported the sudden loss of the ability to generate visual images. He had a significantly lower score in VVIQ (Marks, 1973) compared to his age, gender and IQ-matched controls. But he performed normally on a wide range of mental imagery tasks and other cognitive tasks, except on MR assessed by means of the typical cube stimuli. He was accurate in this task but showed a non-linear pattern in RTs of rotation angle. According to his debrief, he attempted to match individual cubes and angles perceptually before responding, using a strategy different from that of the controls (Zeman et al., 2010).

In line with this observation, in Logie et al.'s experiment (2011), participants were grouped as higher and lower VVI individuals according to their self-reported VVIQ score (Marks, 1973) and were assessed with Shepard and Metzler's typical MR task. Individuals with lower VVI showed a much lower accuracy compared to those with higher VVI, suggesting that the task is more difficult for lower than higher VVI individuals. As the author interpreted, this difficulty may result from lower VVI individuals using a non-optimal strategy which is prone to error (for a discussion see Logie, Cocchino, Della Sala & Baddeley, 2004). In addition, different brain areas were detected as activated in higher and lower VVI individuals, especially in motor related areas: individuals with higher VVI showed more activation than those with lower VVI in premotor cortex while lower VVI individuals showed greater activation in their supplementary motor area (SMA) than did the higher VVI individuals. Although premotor area and SMA were both involved in computing rotation (Leek & Johnston, 2009; Richter et al., 2000; Zacks, 2008), it was suggested that the two areas play a different functional role (Boccardi, Della Sala, Motto & Spinnler, 2002; Toni, Schluter, Josephs, Friston & Passingham, 1999): SMA is responsible for internal-generated actions whereas premotor cortex is responsible for "responsive movements" generating in response to external stimuli (Della Sala & Marchetti, 2005). According to this, the differential brain activation between higher and lower VVI individuals was interpreted suggesting different strategies adopted by different groups in MR tasks.

1.5 Ageing effect in Mental Rotation

The effects of ageing on the MR process have been largely documented by behavioural research (Band & Kok, 2000; Cerella, Poon & Fozard, 1981; Jacewicz & Hartely, 1987; Thomas, 2016). Older adults are consistently found to perform as well as younger adults in familiar object rotation (Cerella et al., 1981; Jacewicz & Hartley, 1979; 1981) but showed deficits in MR tasks with unfamiliar 2D and 3D objects (Gaylord & Marsh, 1975; Puglisi & Morrell, 1986). By analysing the functional brain networks of younger and older adults during a MR task, Thomas (2016) stated that the cognitive deficit in older adults is associated with structural decline, especially in frontal and parietal cortex. The intrahemispheric networks global and local efficiency in the left frontal and left and right parietal areas was reduced with age, whereas in frontal and parietal interhemispheric networks cost efficiency was decreased.

On the other hand, older participants were consistently found to spend longer times than younger individuals in MR tasks (Dror & Kosslyn, 1994; Saimpont, Pozzo, & Papaxanthis, 2009), though the typical linear increase pattern in RTs across rotation angle was also observed (Band & Kok, 2000; Borella et al., 2014). However, as a sequence of five sub-processes underlying the MR task, age-associated decline could result from changes in one or more of these phases. The following section will summarize how age affects MR processing from two aspects, the non-rotation process and the pure MR process, indicated by the estimated intercept and slope in RTs function respectively.

1.5.1 Ageing effect on non-rotation processes

A larger intercept was observed in older adults (Dror & Kosslyn, 1994; Saimpont et al., 2009). This larger intercept could reflect age-related delay in two cognitive processes: a delay either in the early stimuli identification/encoding phase or in the late phase of decision making, or indeed in both these two sub-processes. The effect of age on the object perception, the sub-process occurring before the onset of MR processing has been detected. Norman, Bartholomew and Burton (2008) assessed younger and older adults with 3D objects presented in a series of rotation angles; the participants' task was to distinguish whether the stimuli were the same or not. In processing static 3D objects (without rotation), older adults performed as well as younger participants, whereas they were poorer in identifying the rotated three-dimensional objects. Although ageing deficit in visual perception is widely documented, whether/ how ageing affects the two-dimensional object perception in static and motion status in MR processing is unclear.

1.5.2 Ageing effect on the pure MR process

Age-associated delay was observed in MR rates, indicated by the estimated slope, the other mathematical component in the RTs function. However, the finding of this age-related slowing is contradictory: some studies found a larger slope (equivalent to slower MR rate) in older adults (Cerella, Poon & Fozard, 1981; Gaylord & Marsh, 1975), and other results suggested no ageing effect in the pure MR process by observing no age-related difference in the MR slopes (Jacewicz & Hartley, 1979). Jacewicz and Hartley (1987) assessed three groups of participants with letters, younger

adults, late-middle-age with a mean age of 56 and older adults with a mean age of 68. They did not find a significant difference between the young and middle-late groups in MR processing. But older participants were found to have a slower MR rate in processing these alphabetic letters compared to the other two groups. Based on this result, they explained why they did not find the ageing effect in MR in their previous study (1979) and claimed that such age-related delay in MR does not begin to have an effect until the sixth decade of life.

Stimulus familiarity has been postulated as another possible explanation for this inconsistency (Jacewicz & Hartley, 1987; Hertzog & Rypma, 1991). Different cognitive processes as different mixtures of visual and spatial working memory (WM) (Kosslyn & Thompson, 2000) are suggested to underline MR tasks with different types of stimuli varying in their familiarity (Bethell-Fox & Shepard, 1988; Robert & Bell, 2003); ageing may affect some processes but not others. For example, a canonical object needs to be retrieved from the long-term memory in MR tasks with familiar objects (e.g. alphabetic letters), whereas participants need to encode unfamiliar stimuli first before they actually mentally rotate the corresponding representation in their minds' eyes.

Recently, Hyun and Luck (2007) utilized a dual-task paradigm and found that visual but not spatial working memory (WM) tasks interfered with letter MR tasks, suggesting that visual not spatial WM works as a substrate in processing familiar letters. In this context, older adults could perform as well as, and as fast as, young

adults in familiar object rotation tasks only if their visual WM remains. On the other hand, spatial WM was found to participate in some but not other tasks (de Vito, Buoncore, Bonnefon & Della Sala, 2015; Postle, Idzikowski, Della Sala, Logie & Baddeley, 2007). Therefore, it is possible that spatial WM is not involved in familiar objects processing but participates in the MR tasks with unfamiliar objects. If this were the case, spatial WM which is suggested to enable us to encode and mentally represent the spatial information of objects in space in visual imagery tasks (Logie, 2011; Kosslyn & Thompson, 2000) may possibly store the location of the representation of the unfamiliar stimuli while rotating. Therefore, the declined spatial WM with age may account for the deficit in MR tasks with unfamiliar stimuli.

Alternatively, different strategy selection between younger and older adults was suggested to explain the age-related slowing in MR tasks (Dror Schmitz-Williams & Smith, 2005). To my knowledge, only one study to date has explicitly manipulated the effect of stimulus complexity with the aim of investigating the rotation strategies employed by younger and older individuals. Dror et al. (2005) assessed the performance of younger and older participants in a MR experiment with two-dimensional (2D) drawings of familiar objects (e.g., a helicopter or a house) with different levels of complexity. Stimulus complexity was quantified by calculating the compactness of the drawing (see e.g., Podgorny & Shepard, 1983). Simpler stimuli had a higher compactness value while more complex stimuli had a lower compactness value. Younger participants used a holistic strategy in processing simple objects but

swapped to a piecemeal transformation in processing complex ones, showing a steeper slope. On the contrary, older participants processed both simple and complex objects in a similar manner. The authors interpreted this lack of complexity effect in older participants as evidence that they maintained a holistic strategy while processing both simple and complex objects, because this strategy poses less demands on cognitive resources, including their ability to memorize and mentally manipulate the objects.

1.6 MR Processing for Normal and Mirror Images

Distinctive MR processes were suggested for normal and mirror objects as indicated by behavioural and ERPs as well as patient studies (Hamm et al., 2004; Martinaud et al., 2016; Shepard & Metzler, 1971). Longer RTs were consistently reported in mirror conditions compared to normal ones in MR tasks with three-dimensional (3D) objects (Just & Carpenter, 1976; Shepard & Metzler, 1971), two-dimensional (2D) figure pairs (Cooper, 1975) or individual character letters or digits (Cooper & Shepard, 1973; Corballis, & McMaster, 1996; Hamm, Johnson & Corballis, 2004; Kung & Hamm, 2010). In addition, the onset of RRN ERPs was detected as being delayed in mirror conditions as compared to those in normal ones (Hamm et al, 2004; Núñez-Peña & Aznar-Casanova, 2009). More recently, Martinaud and colleagues (2016) found a classical double dissociation between mirrored and rotation stimuli processing, with one patient presenting a truly selective agnosia for mirrored stimuli and two patients a truly selective orientation agnosia. All these results

suggested the cognitive process underlying the MR processing for mirror stimuli is different from that for normal objects. However, how normal stimuli processing is different from mirror objects at each sub-process in MR tasks is still unclear.

1.6.1 Normal-mirror difference before MR processing

Normal-mirror difference was observed in the stimuli perception, the initial sub-phase in MR processing. In a combined fMRI-eye tracking-study (Paschke et al., 2012), normal and mirror stimuli induced different saccade amplitude, a useful parameter reflecting mental workload (May et al., 1990). Referring to previous literature (Edwards & Goolkasian, 1974; Mackworth, 1965; Plainis, Murray & Chauhan, 2001; Williams, 1989), the smaller saccade amplitude in mirror conditions observed in Paschke et al.'s experiment (2012) indicated a smaller functional field of view for mirror than normal stimuli. This result corresponds to the neuroimaging findings: mirror stimuli processing led to less activation in parts of early visual cortex as compared to that in processing normal objects (Paschke et al., 2012).

In addition, the normal-mirror discrepancy was found in the sub-process of object discrimination in MR tasks. Information about rotated angle and the identity of object is suggested to be processed differently according to the classical visual dual pathway model first proposed by Ungerleider and Mischkin (1982) and expanded or revised since then (Kravitz, Saleem, Baker & Mishkin, 2011; Kravitz, Saleem, Baker, Ungerleider & Mishkin, 2013; Milner & Goodale, 2008; Whitwell, Milner & Goodale, 2014): (1) the 'ventral' pathway involves the occipito-temporal cortex and permits the

identification of visual stimuli (Haxby et al., 2001); (2) the 'dorsal' pathway involves the occipito-parietal cortex and permits the identification of the rotation angle of the visual stimuli (Ng et al., 2001; Niimi, Saneyoshi, Abe, Kaminaga & Yokosawa, 2011).

More recently, a classical double dissociation was found between the discrimination for rotated and mirrored objects as revealed in a patient study (Martinaud et al., 2016). In their study, thirty-four patients with parietal lesion were recruited and assessed with the Mirror and Orientation Agnosia Test (MOAT), an experimental test designed to test agnosia (Martinaud et al., 2014). Twenty patients (59%) had a deficit on the mirror condition. Moreover, one patient presented a selective inability in discriminating between mirror images (also called 'agnosia for mirror stimuli') and two patients an inability in discriminating between objects rotated in the picture plane (also called 'orientation agnosia'). This result strengthened the idea that the mechanism underlying the discrimination for rotated objects is different from that in discriminating the mirrored ones, though single dissociations have been noted with four selective cases of agnosia reported for mirrored stimuli (Davidoff & Warrington, 2001; Martinaud et al., 2014; Priftis, Rusconi, Umilta & Zorzi, 2003; Tumbull & McCarthy, 1996) and one case of orientation agnosia (Turnbull et al., 1997).

1.6.2 Normal-mirror difference in MR processing

A lot of attention has been paid to the pure process of MR in terms of the normal-mirror difference (Hamm et al., 2004; Murray, 1997; Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017). The prolonged RTs in the mirrored condition was

proposed due to the additional sub-process that the mirror image not only needs to be rotated along with the picture plane, but also out of the picture plane to fully normalize it (also called “flip-over”; Murray, 1997). Whereas the MR rate in flipping sub-process was found faster than the rate within the picture plane (Murray, 1997), similar scale distribution of the normal-mirror ERP different waves was found in response to upright letters and those for stimuli with rotated angles (Hamm et al., 2004). This result suggested that a cognitive process similar to within-plane rotation is required to process the upright mirror letters. Moreover, the additional RTs in the mirror condition was found to be correlated with individual MR rate (Hamm et al., 2004; Kung & Hamm, 2010). In their interpretation, this finding indicated that, for example, subjects with slower MR rate (steeper slope) tended to proceed longer in the additional process in flipping the mirrored image over the picture plane. Quan et al. (2017) conducted a more detailed examination and found the RTs difference between normal and mirror stimuli was correlated with individual’s MR rate in normal stimuli only but not for the mirrored ones.

In addition, in a series of ERPs studies, a negative-going component was found by comparing the RRN difference waves between the RRN elicited by normal and mirror stimuli (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009). This component was suggested to be associated with the additional “flip-over” process in dealing with mirrored images and cancelled the plane-rotation RRN in the mirror condition which could be accounted for by the delayed RRN observed in mirror as

compared to that in normal stimuli (Núñez-Peña & Aznar-Casanova, 2009). ERP_{RT} and ERP_{onset} indicated the early and late MR processing phase respectively. Quan et al. (2017) found the rotation angle effect on both ERP_{RT} and $ERP_{onset.}$ But this angle effect could be a better fit for ERP_{onset} with a linear trend than ERP_{RT}, suggesting that the early phase of MR processing is more likely to be representing the rotation within picture-plane (Quan et al., 2017). Moreover, the correlation of ERP_{RT} and RT was found to be more stable in normal condition than in mirror condition (Quan et al., 2017), suggesting that the out-of-plane "flip-over" process is more likely to occur in the late phase.

1.6.3 Normal-mirror difference after MR processing

Cooper and Shepard (1973) suggested that the normal-mirror difference results from the early preparation for 'normal' response at the beginning of a trial. Due to this assumed response bias, longer RTs are required to inhibit the prepared response and to execute an unprepared 'mirror' response. Therefore, one could expect less accuracy in mirror condition as reported by Corballis and McMaster (1996), though no difference in accuracy detected in some others (Cooper & Shepard, 1973; Hamm et al., 2004; Kung & Hamm, 2010).

1.6.4 An example: normal-mirror discrimination with individual letter

The normal-mirror discrimination for individual character letter is a particular example. Due to the different familiarity between a canonical letter and its mirrored

version, it was suggested that there are different MR processes underlying canonical and mirrored letters (Koriat & Norman, 1985). As typically observed MR tasks with two- or three-dimensional unfamiliar objects (Cooper & Podgorny, 1976; Shepard & Metzler, 1971), a linear increment of RTs were observed with increasing rotation angles in processing mirrored alphabetic letters. However, RTs in processing rotated canonical letters was not purely linearly increased with rotation angle but could also be fitted for a quadratic trend, indicating relative indifference to small departures (Cooper & Shepard, 1973; Corbllis & Mclaren, 1984; Corballis & McMaster, 1996; Heil, Rauch & Hennighausen, 1998). The proposition that the nonlinearity effect stems from the extensive experience with alphanumeric characters (Cooper & Shepard, 1973; Kosslyn, 1980; Young, Palef & Logan, 1980) was supported by a training experiment (Koriat & Norman, 1985).

In Koriat and Norman's experiment (1985), participants were trained with unfamiliar nonsense characters with either their canonical or mirror versions. Non-linear pattern was shown in normal condition for participants who had extensive experience of the canonical characters. In addition, the non-linear pattern of RTs was also observed in processing mirror characters after the corresponding training on these types of stimuli. These findings were interpreted as suggesting that the non-linear effect could not only be accounted for in terms of characteristics that are inherent in the visual stimuli, but also rely on the participants' visual experience, that is, on the manner in which the stimulus is represented in the memory. According to Koriat and

Norman (1985), extensive visual experience helps one in establishing a broadly tuned internal representation.

This speculation could be further accounted for by the literature in object recognition. Recognition is achieved by the use of transformation processes to convert an input representation of an object at its current orientation to a canonical orientation at which the memory representations are stored, or to transform memory representations into the orientation of the input shape (Tarr & Pinker, 1989). For children who have no experience of character letters, no representation of these letters was expected to be stored in their memory. It is a normal to observe children as making more errors in mirror reading and writing (Cornell, 1985; Cubelli & Della Sala, 2009; Dehaene et al., 2010; Schott, 2007). This challenging problem was suggested as resulting from the "mirror invariance" phenomenon, an ability which enables one to recognize images which are indifferently seen from a left or right perspective (e.g. left or right profile of a predator) and silhouettes of objects seen from opposite sides (Cornell, 1985; Pegado, Nakamura, Cohen & Dehaene, 2011; Schott, 2007). Due to the fixed orientation of letters in the Latin alphabet and the presence of minimal pairs such as "p" and "q", mirror invariance is an unavoidable property for children at the beginning of reading and writing. But after the acquisition of these skills, the children then have the ability to recognize with longer times required to recognise mirrored letters than normal ones (Cornell, 1985; Pegado, Nakamura, Cohen & Dehaene, 2011; Schott, 2007).

1.7 Structure of the Thesis

We present the thesis so that it gives answers to the principal question: whether and, if so, in which contexts the different strategies are adopted in MR tasks. Encompassing this question, eight experiments were conducted to explore this possibility in both younger and older adults. Throughout this thesis, MR is considered as a complex cognitive process involving rotation process proper and other non-rotation process (es) in which individuals may vary in one or the other.

Chapter 2 presents three experiments to explore the role of visual imagery ability in cognition by investigating how individuals with different visual imagery ability performed on MR tasks. We use VVIQ2 in these experiments to measure individual's visual imagery ability. In Experiment 1, we employ a behavioural MR paradigm to demonstrate in which context and how individuals performed differentially in MR tasks. Thirty-six participants were recruited in a series of MR tasks with different complexity. We illustrate the group difference by comparing the performance between higher (with high VVIQ2 score) and lower VVI individuals (with low VVIQ2 score). Moreover, we specify the strategy selection in each imagery group under different task demand based on the exploration of the stimulus complexity effect in each group. The results are discussed drawing reference to the specified strategy selection under different MR task demands. Moreover, we discuss these results in the light of the inconsistences in literature in individual difference in MR as

regard to spatial ability, and offer the explanation challenging the speculation on the correspondence between high/low spatial ability and good/poor representation skills

The follow-up ERP experiment (Experiment 2) further explores the neural mechanism of how visual imagery ability affects MR processing. In this experiment, we employ the ERPs paradigm with a standard letter rotation task. On a sample of eighteen higher and eighteen lower VVI individuals, the time course of MR processing was directly compared between higher and lower VVI individuals in normal and mirror conditions to test the neural correlates between visual imagery and the MR processing. We discuss the results in the view of how visual imagery ability affects the MR performances.

In Experiment 3, we report the single case (M.X.) who reported the sudden loss of his visual imagery ability, to test whether MR tasks could be completed in the absence of visual imagery. By using the same ERP paradigm, we compare the neural correlate of MR processing was directly compared between M.X. and his age, sex and IQ-matched controls ($N = 11$). The results are discussed encompassing the issue on the functional role of visual imagery in MR tasks, and we offer explanations and possibilities on how MR process could be completed in the absence of visual imagery in terms of the usage of non-depictive representation and other possible strategies in MR tasks.

In Experiment 4, as presented in Chapter 3, we move on to test the hypothesis that multiple formats of visual representations and strategies could be adopted in MR

from another point of view- whether multiple strategies could be adopted in different types of stimuli in this experiment. We first address this issue by assessing the research question: which properties of the visual stimuli predict the strategy selection in MR tasks. In order to test this hypothesis, participants ($N = 22$) were assessed with a series of MR tasks with different types of stimuli. The influences of two properties of the visual stimuli, the segment number and vertices number on strategy selection in MR tasks are discussed based on the stimulus complexity effect on the different types of stimuli. In addition, the distractors were introduced as typically used in previous studies investigating stimulus complexity hypothesis by assuming these distractors could enforce participants to encode all the information of the stimuli. We then discuss this functional role of the distractors in MR task by comparing the stimulus complexity effect in with-foil and without-foil conditions.

In Chapter 4, we present three experiments to look at the ageing effect on MR performance. We present the first two experiments (Experiments 5 & 6) focusing on the potential ageing effect on the pure rotation process proper. We employ the MR tasks with unfamiliar three-dimensional (3D) objects in Experiment 5 based on a sample of nineteen younger and nineteen older participants and explore the strategy selection in younger and older adults. In Experiment 6, another twenty younger and twenty older participants were recruited and assessed with MR tasks with unfamiliar two-dimensional (2D) objects. We then discuss the results in the view of whether the widely documented age-associated slowing in MR rate could be accounted by the

different strategy selection. Moreover, we offer possible reason in the light of the contrary findings to the previous MR experiments with familiar objects.

Experiment 7, on the other hand, explores the potential ageing effect on non-rotation processes in MR tasks. We employ the ERPs paradigm with a standard letter rotation task and compare the time course of MR processing between younger ($N = 13$) and older participants ($N = 13$). The results are discussed demonstrating that one source of the age-related slowing observed in previous behavioural MR tasks is linked to the initial phase before the MR process proper occurs.

In Chapter 5, we present a detailed analysis of MR processing with normal and mirror objects in Experiment 8 to present the temporal relationship of the planar and non-planar rotation which was explored for different rotation angles.

Finally, in Chapter 7, we review the key findings of these eight experiments conducted as a part of this thesis. We then discuss these results encompassing four themes on 1) how visual imagery affects the MR performances; 2) in which context the multiple strategies could be adopted in MR tasks; 3) our re-examination of the largely documented ageing effect in MR tasks and 4) the time course of planar and non-planar rotation for different rotation angles. In each theme, we discuss these results in the context of the existing literature and highlight the main methodical and empirical contributions of the research. The suggestions for potential future investigations are provided as well.

Chapter 2

Individual Difference in Mental Rotation

This chapter tests the hypothesis that individuals who differ in their vividness of visual imagery (VVI) could adopt different representations and different strategies in the same MR task. To test this hypothesis, the performances between higher and lower VVI individuals were directly compared in the first two experiments and one more experiment testing the single case, an imagery impaired patient. In the first experiment, a behavioural paradigm was used. In this behavioural experiment, individual difference in strategy selection in MR tasks was tested by examining the estimated slope in RTs function of rotation angle according to Cooper's stimulus complexity hypothesis (1975; see also Cooper & Podgorny, 1976; see Figure 1-3). In the following two experiments, EEG was recorded while participants were performing a standard letter rotation task. The pattern of rotation-related negativity (RRN) was analysed between groups to address whether differential neural mechanisms

underlying MR processing for higher and lower VVI individuals (Experiment 2) as well as between the visual imagery impaired patient and his age, sex and IQ matched controls (Experiment 3).

In all these three experiments, the visual imagery ability was assessed by VVIQ2 (Marks, 1973; 1995) (Appendix A). As introduced in Chapter 2, VVIQ2 is a standardised questionnaire assessing general visual imagery use and experience (Pearson, Deeprose, Wallace-Hadrill, Heyes & Holmes, 2013). Participants were instructed to close their eyes to imagine 32 items (e.g. a scene, an event or an object) and to rate the vividness of the image generated in their minds' eyes from five levels, namely "perfectly clear and as vivid as normal vision", "clear and reasonably vivid", "moderately clear and vivid", "vague and dim" and "no image at all, you only "know" that you are thinking of an object".

The reason we chose visual imagery vividness is because this ability was found to affect the visual perception ability (Pearson et al., 2008) and positively correlated with the format of mental representation mainly indicated by the V1 activation (Reeder, 2017; Cui et al., 2007; Lee et al., 2012; Olivetti Belardinelli et al., 2009). For example, participants were asked to imagine themselves or another person in an fMRI study (Cui, et al., 2007). The early visual cortex activity relative to the whole brain activity measured by fMRI was found highly correlated to participants' subjective rating on VVIQ2.

More recently, the level of visual imagery vividness was also suggested may mediate different strategy selection in MR tasks. M.X., a 65-year-old retire surveyor is such an example for this issue and well documented in Zeman et al.'s study (2010). M.X. reported his sudden loss of his visual imagery ability and showed a significant lower VVIQ score as compared to his age, sex, and IQ-matched controls. He performed normally on a wide range of mental imagery tasks including a MR task assessed with Shepard and Metzler's typical arm-like cube objects (1971). Interestingly, though he performed as well as his controls in this MR experiment but he did not show the typical linear pattern in RTs function of rotation angle while his controls did. As he debriefed, he used an alternative strategy instead of rotating the stimuli as whole in his mind throughout the experiment. In line with this idea, higher and lower VVI individuals were assessed with the same arm-like cube rotation task in an fMRI study (Logie et al., 2011). Differential brain areas were found activated for higher and lower VVI individuals, suggesting different strategies adopted by different groups in MR tasks.

2.1 Experiment 1

2.1.1 Introduction and brief recap

As discussed in the opening chapter, the stimulus complexity effect on the estimated slope measures in RTs function of rotation angle was suggested could indicate the strategy selection in MR tasks (Cooper, 1975; Cooper & Podgorny, 1976).

According to Cooper's speculation (1975; see also Cooper & Podgorny, 1976), as depicted in Figure 1-3, MR rate (suggested reflected by the estimated slope measure in RTs function) should depend on the rotation angle only in holistic processing, whereas MR rate is not only dependent on the rotation angle but also the stimulus complexity when participants rotated the stimuli piece-by-piece. In addition, a shallow slope would be expected when participants automatically simplify the task by representing partial image of the stimuli in their minds and rotating such to complete the task. Based on this hypothesis, the first experiment we conducted to explore the individual differences in strategy selection in MR.

To test this complexity effect hypothesis, Cooper and Podgorny (1976) used 2D polygons as their visual stimuli with different complexity levels manipulated by the number of vertices (Attneave & Arnoult, 1956). No effect of complexity was observed in this experiment, supporting the idea that a holistic strategy was at play. Some other researchers, however, did observe this complexity effect by replicating Cooper and Podgorny's experiment (1976) using polygons (Folk & Luce, 1987) or 3D cube figures as stimuli (Bethell-Fox & Shepard, 1988; Yuille & Steiger, 1982), hence, supporting the piecemeal transformation hypothesis.

It has been argued that the failure to generate the complete image in internal representations leads to the lack of the complexity effect even if piecemeal transformation is at play (e.g., Cooper & Podgorny, 1976; Folk & Luce, 1987). It has been posited that participants have the ability to maintain a simplified representation

of the stimuli rather than the whole image and rotate such precise representation in their mind's eye (Liesefeld & Zimmer, 2013), especially when the stimuli are complex (Yuille & Steiger, 1982). Such precise representations permit a faster MR rate and result in a shallower RTs slope (Mumaw, Pellegrino, Kail & Carter, 1984; Yuille & Steiger, 1982).

The different methods of manipulating stimulus complexity is another possible reason for the inconsistent results gleaned from the literature. Two methods were used to manipulate the stimulus complexity: 1) the number of components of an integrated object, like the number of vertices in polygons (e.g., triangles, polygons with 6, 9, 12 points; Cooper, 1975; Cooper & Podgorny, 1976; Folk & Luce, 1987) or the number of shaded squares in matrices (Bethell-Fox & Shepard, 1988); 2) the number of perceptually distinct pieces, like the figure patterns (1, 2, or 3 pieces) in matrices (Bethell-Fox & Shepard, 1988; Podgnory & Shepard, 1983) or the number of segments in Shepard and Metzler's (1971) typical cube figures (Yuille & Steiger, 1982). The lack of the effect was mostly observed when complexity was manipulated within one integrated object (e.g., Cooper, 1975; Cooper & Podgnory, 1976); it has been suggested that participants are more likely to operate piecemeal transformation in processing the stimuli consisting of several parts (Bethell-Fox & Shepard, 1988).

Our aim in the present experiment was to investigate the individual differences in imagery tasks. We hypothesised that individuals differing in their imagery abilities may create different formats of visual images under different task demands and utilise

these multiple visual representations to generate different strategies for further mental manipulation. Higher and lower VVI individuals may not differentiate in processing an integrated object, but would show differences in processing objects consisting of several pieces.

For the purpose of the current study, the stimulus complexity level was manipulated in two ways: 1) the cube number in an integrated object; 2) the segment number of the stimuli. Accordingly, higher and lower VVI individuals were grouped and assessed with four types of stimuli: two Standard and two non-Standard cube objects. We selected Shepard and Metzler's (1971) typical objects (Figure 2-1a) as the basic Standard stimuli, the same types of stimuli used in the studies with MX (Zeman et al., 2010; Logie et al, 2011). The other Standard objects comprised a series of eight-cube stimuli (Figure 2-1b). In non-Standard objects, one set consisted of two segments (Figure 2-1c) and the other set of three segments (Figure 2-1d).

The effect of cube number was tested to explore the individual differences in processing an integrated object by comparing the two Standard objects (Figure 2-1a and 2-1b). If participants transformed the object cube by cube, more time would be needed and a steeper slope should be observed in RTs in the ten-cube object. If instead a holistic strategy is applied, no time difference should be observed between objects and no effect of cube number is predicted. According to the behavioural results reported by Logie et al. (2011), we predicted that no effect of cube number on the slopes would be found in the Standard condition for both higher and lower VVI

individuals that both of the groups would tend to use holistic strategy. This result will be used as a baseline for future analysis of the effect of segment number.

The effect of segment number was analysed to investigate whether individuals differ in processing objects consisting of several parts by comparing three types of stimuli: eight-cube Standard (Figure 2-1b), two-segment and three-segment non-Standard (Figure 2-1c and 2-1d). The eight-cube Standard objects served as control for the effect of cube number compared with the non-Standard objects which also consisted of eight cubes. If participants used piecemeal transformation for the non-Standard objects, they should have slower and less accurate performance with these figures than the Standard ones, assuming that the Standard objects can be rotated holistically. If a precise internal representation of the non-Standard object was generated for MR processing, participants would perform faster and more accurate in these objects than the Standard one in which holistic strategy is assumed to be applied. We predicted that individuals with higher VVI will be more flexible in manipulating their visual representations and would represent more precise images for more complex stimuli and rotate them more efficiently by showing a shallower slope in their RTs. On the other hand, individuals with lower VVI might have difficulties in representing the whole non-Standard images and would transform the stimuli piece-by-piece by showing a steeper slope in their RTs functions in the non-Standard condition.

2.1.2 Method

2.1.2.1 Participants

Thirty-six university-level students were recruited in this experiment. Two were excluded due to their low accuracy ($< 50\%$). Therefore, thirty-four data from students aged 21 to 36 years (average age $= 26.2$ years; 16 female) were analysed. All participants were right-handed, with no history of neurological disorders and reported having normal or corrected-to-normal vision.

Participants were classified as higher and lower VVI individuals based on their performance in the VVIQ2 (Marks, 1999). The VVIQ2 scores ranged from 76 to 144 out of a possible total of 160 (mean $= 110.72$, SD $= 17.47$) and were normally distributed. Based on the VVIQ2 performance, nine higher (top VVIQ2 score quartile, mean $= 133.11$, SD $= 6.21$, six men and three women, mean age $= 24.56$ years) and nine lower VVI individuals (bottom VVIQ2 score quartile, mean $= 90$, SD $= 6.38$, six men and three women, mean age $= 26.44$ years) were selected for further analysis.

2.1.2.2 Stimuli

The stimuli were arm-like stimuli formed of cubes derived from Shepard and Metzler (1971). Four types of stimuli were used in the present MR task, two Standard and two non-Standard. One set of Standard stimuli (Figure 2-1a) was exactly the same as the one used in Shepard and Metzler (1971) which consisted of ten cubes. The other set of Standard stimuli (Figure 2-1b) consisted of eight cubes. Similar to the 'fragmented' stimuli in Khooshabeh et al.'s experiment (2013), both types of non-Standard stimuli (Figure 2-1c and Figure 2-1d) were devised by withdrawing two

cubes from the Standard stimuli (Figure 2-1a) used in Shepard and Metzler's experiment (1971). The difference between these two non-Standard stimuli was the number of segments involved: One set was devised by withdrawing two consecutive cubes from the Standard stimuli (Figure 2-1c); the other was concocted by removing two non-consecutive cubes (Figure 2-1d).

For each type of stimuli, a pair of objects was set as a trial with different rotation angle, between 0° and 180° with 20° increments (10 rotation angle), in which half the stimuli were rotated along with the picture plane and the others rotated in depth (two axis). Within half of the trials, one object was paired with an exactly identical corresponding object with a different orientation, whereas the other half was set with its mirrored figure but still had a different orientation (two identities). There were 160 trials (4 types of stimuli $\times 10$ rotation angle $\times$ 2 identities $\times$ 2 rotate axis $=$ 160 trials) with ten repetitions of each stimulus randomly ordered. Accordingly, in total 1600 trials were included in this four-block experiment with 400 trials in each block.

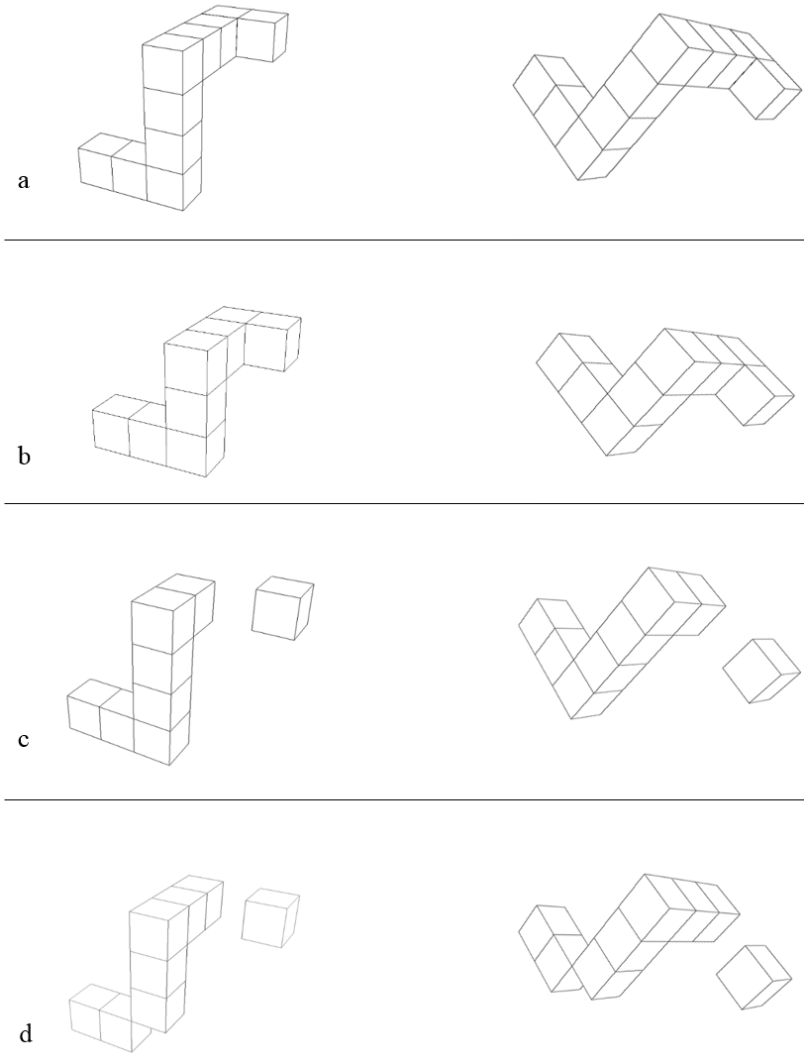

Figure 2-1. The four types of stimuli used in Experiment 1. Figure 2-1a and Figure 2-1b examples of the two Standard stimuli. One is the typical ten-cube object (Figure 2-1a) whereas the other is composed of eight cubes (Figure 2-1b). Figure 2-1c and Figure 2-1d examples of the two non-Standard stimuli designed by withdrawing two cubes from the Standard stimuli. One set was designed by withdrawing two consecutive cubes (Figure 2-1c), whereas the other set (Figure 2-1d) was designed by withdrawing two non-consecutive cubes.

2.1.2.3 Procedure

The participants were required to sit in front of a computer with the keyboard all masked except for two buttons marked “S” and “D”, indicating “same” and “different” respectively. For half of the participants, the “S” button was set on their right hand side and the “D” button on their left side. For the other half of the participants, the “S” button was set on their left side and the “D” on their right.

A run-in of 16 trials served as practice allowing participants to familiarise themselves with the task. In both the practice and real experiment sessions (see Figure 2-2), first a black screen was presented for 250ms, followed by a fixation cross lasting 1,000ms to 1,200ms then a pair of 3D cube stimuli were presented for 6,500ms. Participants had to indicate whether these two objects were the same ones (though rotated) or mirror images by pressing the “S” or “D” button. During the whole procedure, the participants were asked to keep their hands on the keyboard. Each experimental block was followed by a debriefing session, in which participants orally reported on the strategy they used in the previous block.

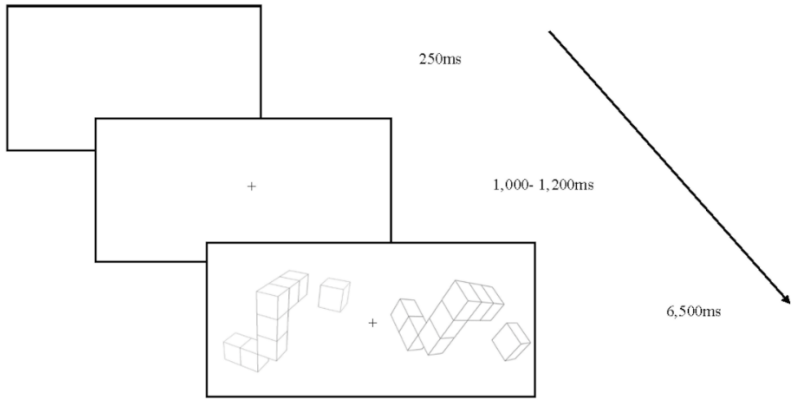

Figure 2-2. The experimental procedure in Experiment 1.

2.1.2.4 Data Analysis

Prior to the analysis, RT data were trimmed for outliers. RTs more than two standard deviations above or below the mean per condition and per subject were excluded (3.7% of the data on average). As presented in the literature review that distinctive neural mechanism underlying normal and mirror rotations (Martinaud et al., 2016), the results were analysed based on the normal trials only, as did in previous studies in strategy selection in MR (e.g. Heil & Jansen-Osmann, 2008; Khooshabeh, Hegarty & Shipley, 2013).

A repeated-measures analyses of variance (ANOVAs) was applied to the corrected RTs as well as accuracy data with one between-subject factor (higher or lower VVI individuals) and two within-subject factors: types of stimuli with different complexity levels and ten rotation angles. When imagery ability was found interacting with types of stimuli or rotation angle, independent t-tests would apply to test group difference (higher vs. lower VVI individuals). Trend analyses would be applied for testing the effect of rotation angle in each condition followed by Bonferroni corrected pairwise comparisons, if rotation angle was observed to interact with other factors.

To test the MR rate under different task demands, we fitted a linear line to each participant's RTs to calculate the slope and intercept of this line. Repeated ANOVA was used for these estimated slope and intercept between two imagery ability groups with different stimulus complexity levels. Independent t-test would apply to test group differences (higher vs. lower VVI individuals) in each type of stimuli when the

interaction of types of stimuli and imagery ability was found. A repeated-measures ANOVAs would again be used for higher and lower VVI individuals separately followed by the Bonferroni corrected pairwise comparisons for testing the complexity effect in each group.

2.1.3 Results

2.1.3.1 Effect of Cube Number

Consistent with previous literature, there was an effect of rotation angle on RTs, F (9, 144) = 56.58, $p < .001$, $\eta^2 = .99$ as well as on the accuracy, F (9, 144) = 34.43, $p < .001$, $\eta^2 = .68$. As expected, both higher and lower VVI individuals did not differ in their RTs on the eight-cube and ten-cube Standard objects, F (1, 16) = .01, $p = .918$, $\eta^2 = .001$, as well as in their accuracy, F (1, 16) = .09, $p = .765$, $\eta^2 = .01$. Moreover, both higher and lower VVI individuals did not differ in MR rate in processing these two Standard objects, F (1, 16) = .05, $p = .834$, suggesting that both higher and lower VVI individuals did not at least transform the object cube-by-cube and may instead have applied a holistic strategy in the Standard conditions.

2.1.3.2 Effect of Segment Number

Response Times

Figure 2-3 details the RTs in all three conditions for both higher and lower VVI individuals as a function of rotation angle. As predicted, there was an interaction between imagery ability and types of stimuli, F (2, 32) = 8.38, $p = .001$, $\eta^2 = .34$.

Group difference was analysed separately in different types of stimuli and indicated that higher and lower VVI individuals did not differ in the Standard stimuli, t (16) = .680, p = .506, but differed in the two-segment non-Standard object, t (16) = -2.24, p = .041 and the three-segment, t (16) = -3.22, p = .005. In processing the non-Standard objects, lower VVI individuals spent much more time (two-segment = 3082.79ms, SD = 665.41; three-segment = 3982.05ms, SD = 801.55) than higher VVI individuals (two-segment = 2473.76ms, SD = 479.42; three-segment = 2892.15ms, SD = 624.38).

As revealed by previous studies, a main effect of rotation angle was observed on RTs for all the types of stimuli, F (9, 144) = 131.57, p < .001, η^2 = .89, which confirmed a linear trend, F (1, 16) = 442.54, p < .001, η^2 = .97. The rotation angle effect was also different in higher and lower VVI individuals, F (9, 144) = 4.97, p < .001, η^2 = .24. For higher VVI individuals, RTs linearly increased with the increasing rotation angle, F (1, 8) = 98.49, p < .001, whereas lower VVI individuals' RTs fit for both linear, F (1, 8) = 351.60, p < .001, η^2 = .98, and quadratic trends, F (1, 8) = 11.12, p = .01, η^2 = .58, though rotation angle effect was observed in both higher, F (9, 72) = 29.54, p <.001, η^2 = .79, and lower VV individuals, F (9, 72) = 33.29, p < .001, η^2 = .81. For individuals with lower VVI, indicated by the Bonferroni correction, RTs were irrelevant to rotation angle in larger rotation angles, raising slightly from 100° (mean = 4202.60ms, SD = 4783.87) to 180° (mean = 4783.87), which were not statistically significant between each of the two consecutive angles,

100°-120° (p =1.000), 120°-140° (p = 1.000), 140°-160° (p =1.000) and 160°-180° (p =1.000). This quadratic-pattern RTs in lower VVI individuals in the present experiment is consistent with what Logie et al. (2011) found in their lower VVI individuals' performance as well as MX's in Zeman et al.'s (2010). These findings suggested that individuals with lower VVI might be impaired in maintaining the quality of their representation for larger rotation angles, which has been proposed by Mumaw et al. (1984) before.

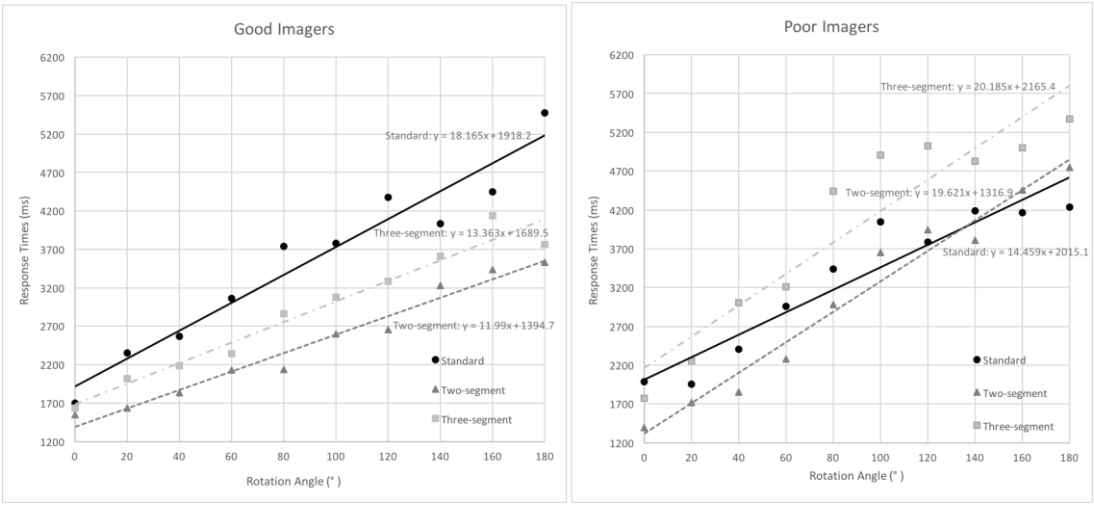

Figure 2-3. RTs as a function of rotation angle in processing the Standard stimuli as well as the two non-Standard stimuli in Experiment 1. The left plot reports the RTs functions for higher VVI individuals; the right plot is the RT functions for lower VVI individuals.

Accuracy

As depicted in Figure 2-4, accuracy rate decreased with the rotation angle, F (9, 144) = 43.66, $p < .001$, $\eta^2 = .73$. Rotation angle effect on the accuracy was also observed in differences between higher and lower VVI individuals, F (9, 144) = 5.01,

$p < .001$, $\eta^2 = .24$, which confirmed a linear trend in both higher, F (1, 8) $= 17.81$, $p = .003$, $\eta^2 = .69$, and lower VVI individuals, F (1, 8) $= 270.33$, $p < .001$, $\eta^2 = .97$. Independent t-tests were applied separately for different rotation angle and we found that lower VVI individuals performed worse than those with higher VVI in larger rotation angles, larger than 100°, which was statistically significantly different at 120° ($p = .036$), 140°($p < .001$), 160° ($p = .016$) and 180° ($p = .023$). As shown in the right panel of Figure 2-4, the accuracy rate of lower VVI individuals reached the chance level in larger rotation angles, suggesting that they might have difficulty in mental manipulation for larger angles.

A main effect of segment number was also observed on accuracy rate, F (2, 32) $= 5.25$, $p = .011$, $\eta^2 = .24$. Participants performed more accurately in the two-segment non-Standard objects (mean $= 86.6\%$, SD $= 9.04$) than the Standard (mean $= 77.0\%$, SD $= 11.2$) and three-segment non-Standard ones (mean $= 81.9\%$, SD $= 11.9$). However, unexpectedly, higher and lower VVI individuals did not differ in these different types of stimuli, F (2, 32) $= 2.43$, $p = .104$, $\eta^2 = .13$.

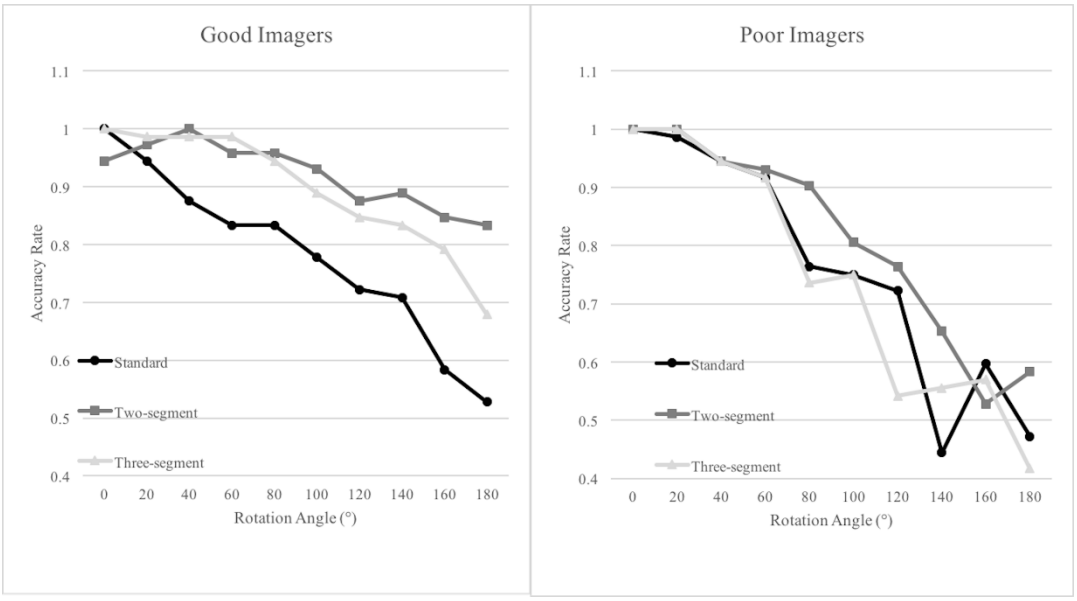

Figure 2-4. The accuracy rate across the rotation angle from 0° to 180° in processing the Standard stimuli as well as the two non-Standard stimuli. The left panel reports accuracy rate across all the rotation angles for higher VVI individuals; the right panel is the accuracy rate for lower VVI individuals.

Slope and Intercept

The most direct test of the predictions outlined above is based on estimates of MR rate (reverse of the slope in RTs). Group difference (higher and lower VVI groups) was found on the slope measure, F (1, 16) = 5.27, p = .036, η^2 = .25, showing that higher VVI individuals (mean = 14.51ms/degree, SD = 4.14) processed the stimuli significantly faster than lower VVI individuals (mean = 18.05ms/degree, SD = 2.85).

As expected, an interaction between imagery ability and types of stimuli was also found in the slope measure, F (2, 32) = 25.45, p < .001, η^2 = .61. Higher and lower VVI individuals did not differentiate in processing the Standard objects (higher

VVI individuals = 18.165ms/degree, SD = 4.75; lower VVI individuals = 14.350ms/degree, SD = 3.10), t (16) = 2.02, p = .258, but showed the group difference in both two-segment, t (16) = -3.91, p = .001, and three-segment non-Standard objects processing, t (16) = -3.957, p = .001. Higher VVI individuals performed much faster (two-segment = 11.99ms/degree, SD = 3.63; three-segment = 13.36ms/degree, SD = 4.04) than lower VVI individuals (two-segment = 19.62ms/degree, SD = 4.59; three-segment = 20.18ms/degree, SD = 3.23) in these non-Standard objects.

A repeated-measures ANOVA was applied to individuals with higher VVI only and the main effect of types of stimuli was found on the slope measure of the RTs of rotation angle, F (2, 16) = 15.79, $p < .001$, $\eta^2 = .66$. As depicted in the left panel of Figure 2-5, a shallower RTs slope was observed in both two-segment and three-segment non-Standard conditions than the Standard one. Post-hoc analyses with the Bonferroni correction indicated that the MR rate in processing the Standard objects (mean = 18.165ms/degree, SD = 4.75) was much slower for higher VVI individuals than that in two-segment and three-segment objects; this difference was statistically significant, in both cases at p = .007. However, in processing the non-Standard objects, individuals with higher VVI performed similarly in the two-segment (mean = 11.99ms/degree, SD = 3.63) and three-segment (mean = 13.36ms/degree, SD = 4.04), p = .493. This shallower-pattern slope is consistent with Yuille and Steiger's

(1982) findings, suggesting that higher VVI individuals might have more precise representation for the non-Standard object and used it for MR processing.

A repeated-measures ANOVA was also applied for individuals with lower VVI. As expected, the main effect of types of stimuli was found on slope for lower VVI individuals as well, F (2, 16) $= 11.05$, $p < .001$, $\eta^2 = .58$. Post-hoc tests using the Bonferroni correction revealed that lower VVI individuals processed the two-segment (mean $=$ 19.62ms/degree, SD $=$ 4.60) and three-segment objects (mean $=$ 20.18ms/degree, SD $=$ 3.23) at a similar MR rate, $p = 1.000$. However, in contrast to higher VVI individuals, as depicted in the right panel of Figure 2-5, a steeper RTs slope was shown in both two-segment and three-segment objects than the Standard one. Lower VVI individuals performed much faster in Standard objects (mean $=$ 14.35ms/degree, SD $=$ 3.10) than in two-segment and three-segment non-Standard objects; this difference was reliable for two-segment ($p = .031$) and three-segment objects ($p = .001$). This slower performance in non-Standard objects is consistent with our prediction suggesting that individuals with lower VVI use piecemeal transformation instead of holistic strategy in processing the multi-part objects.

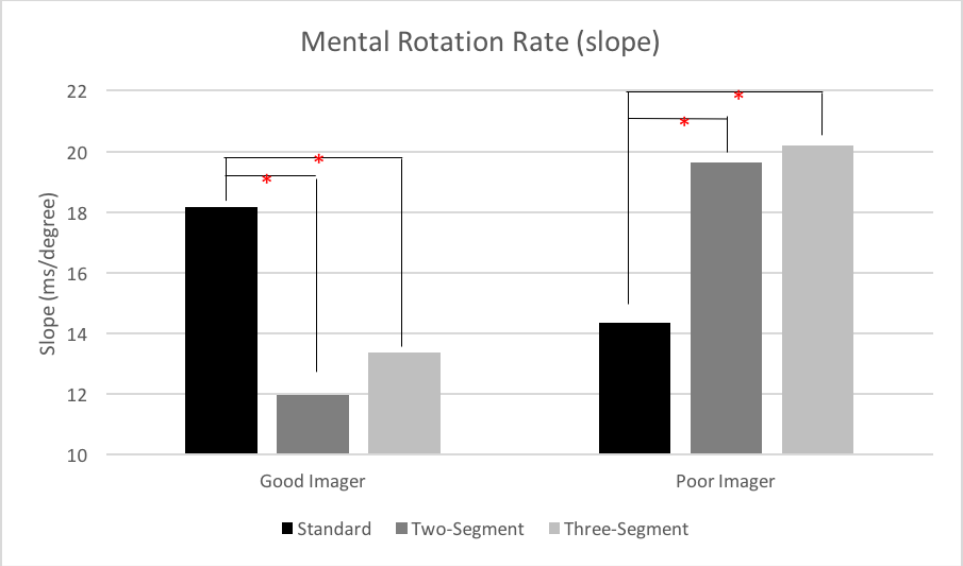

Figure 2-5. The MR rate (slope) for higher (left-side panel) and lower VVI individuals (right side panel).

A main effect of segment number was observed on the intercept measure, F (2, 32) = 9.19, p = .001, η^2 = .37. Participants took significantly less time in encoding the two-segment stimuli (mean = 1300.80ms, SD = 505.56) than the three-segment objects (mean = 1927.43ms, SD = 649.01) and the Standard ones (mean = 1968.01ms, SD = 648.96), p = .011 and .002 respectively. However, the segment number effect was no different between higher and lower VVI individuals, F (2, 32) = .94, p = .402, η^2 = .06, nor the group difference on this intercept measurement, F (1, 16) = 1.00, p = .331, η^2 = .06.

2.1.4 Discussion

By manipulating the complexity of the stimuli, we tested and specified individual differences with regard to visual imagery capacities on performing the MR task with one integrated object (Standard condition) and objects consisting of several segments (non-Standard condition). Higher and lower VVI individuals performed similarly in the Standard objects and showed no cube number effect on either their RTs or estimated slope measure. However, higher and lower VVI individuals differed in processing the multi-part non-Standard objects. Compared with the eight-cube Standard object, individuals with higher VVI performed faster in non-Standard ones whereas lower VVI individuals obtained the opposite pattern of performance.

Consistent with Logie et al.'s behavioural results (2011), in the Standard condition, no effect of cube number was observed on either RTs or slope measure in either higher or lower VVI individuals. This suggests that the same strategy was adopted by both groups and that they did not transform the Standard objects cube-by-cube.

A different pattern emerged from the analyses of the processing of the multi-part non-Standard objects. Here the higher and lower VVI individuals' performance differed; various representation formats and various strategies were observed across individuals. Higher VVI individuals performed faster in non-Standard objects than in the Standard ones. This finding confirmed Yuille et al.'s (1982) precise representation transformation account which maintains that participants could generate a partial image of the stimuli in their mind's eye and rotate it to complete the MR task.

Alternatively, Liesefeld and Zimmer (2013) postulated that only comparison-relevant information was maintained for further holistic MR processing. Here we cannot detail the content of the simplified representation but further specify that only individuals with higher VVI were able to apply this precise transformation in MR tasks.

Lower VVI individuals, on the other hand, showed a steeper slope in RTs in non-Standard objects, suggesting that they used piecemeal transformation to process the fragmented objects. This finding is consistent with the claims that individuals with lower VVI have difficulty in rotating the more complex object holistically (Mumaw et al., 1984). Lower VVI individuals might have difficulty encoding the multi-part non-Standard objects as a unit in their mind's eye. They instead may attempt to encode the non-Standard stimuli as one part attached to another. Given the limitations of our visual system capacity so that only one additional part/information could be maintained attached to another part (Xu & Franconeri, 2015), they might fail to represent the stimuli with multiple parts and have to transform the individual parts separately.

It is notable that lower VVI individuals processed the two-segment and three-segment non-Standard objects at a similar rate. This seems to question the piecemeal transformation account in which more time would be needed for transforming the additional segment in three-segment objects and a steeper slope would be observed in the RT in these objects. One possibility is that individuals with lower VVI attempted to use piecemeal transformation for the non-Standard objects but failed under time

constraint to transform the additional piece in the three-segment objects for larger angles. This account is supported by their low accuracy and angle-irrelevant RTs in larger rotation angles.

In sum, at odds with the simple dichotomies object/spatial or visualizer/verbalizer (Paivio, 1971; Kozhevnikov et al., 2005), the findings from our present experiment support Pearson and Kosslyn's recent argument (2015) that multiple formats of representation could be created and those representations could be flexibly used in further mental manipulations. We specified the format of representation and strategy selection under different tasks across individuals; we observed that there was no individual difference in processing integrated objects, whereas in processing fragmented objects, multiple formats of representations and multiple strategies could be generated across individuals with different levels of visual imagery ability. Individuals with higher VVI are more flexible in generating different formats of representation and particularly in processing more complex objects and they could maintain a precise representation of the stimuli in their mind's eye for further mental manipulations; individuals with lower VVI instead rely more on piecemeal transformation in processing multi-part objects.

2.2 Experiment 2

2.2.1 Introduction and brief recap

In this following experiment, we aimed to further explore the neural correlates between visual imagery vividness and MR processing. Event-related potentials (ERPs) were used in this experiment. Thanks to their high time resolution, they are an effective tool to investigate the time course of the neural mechanism underpinning cognitive processes. In Shepard and Metzler's MR paradigm (1971), two unfamiliar stimuli are presented on each trial and participants had to move their eyes to compare and judge whether these two stimuli are identical or mirror images. To avoid the ocular artifacts in the ERPs data produced by the eye movements, the Cooper and Shepard's paradigm (1973) is typically used in ERP studies of MR. In this task, a single well-learn canonical character is centrally presented on the screen on each trial for a short period of time (typically less than 500ms). Thus, participants are encouraged to maintain fixation throughout the task. Given a linear increase in RTs as a function of rotation angle is typically observed during the rotation of unfamiliar (novel) 2D and 3D visual stimuli (Cooper & Podgorny, 1976; Shepard & Metzler, 1988), studies using well known stimuli such as letters have often observed a curvilinear rather than a linear RT increase (Hamm, Johnson & Corballis, 2004; Milivojevic, Hamm & Corballis, 2011). This observation raised the question of whether the process of MR is engaged during the rotation of familiar stimuli. Cooper and Shepard (1973; see also Koriate & Norman, 1985) suggested that the curvilinear pattern can still be considered reflecting MR, if one assumes that MR does not occur on all trials but only in a proportion of the trial and it is less likely to occur with small rotation angles.

Behavioural measures represent an indirect index of MR because they reflect the end result of different cognitive sub-processes such as character processing, character identification, MR proper, parity judgment and response selection and execution (Heil and Rolke, 2002). Therefore, the question of whether MR proper occurs during the rotation of familiar stimuli has been investigated with different imaging techniques which can provide a direct insight into the brain mechanisms underlying MR (Harris & Miniussi, 2003; Heil, Bajric, Rösler & Hennighausen, 1996; Heil, Rauch & Hennighausen, 1998; Zacks, 2008). In particular, electrophysiological measures were proven extremely useful in the study of MR processes because they can track the time course of cognitive processes with high temporal resolution.

As described in the opening chapter, electrophysiological studies of MR have shown that ERPs elicited over the parietal cortex become more negative with increasing rotation angles between 350-650ms after the onset of the stimulus (Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989; see Heil, 2002, for a review). This 'Rotation Related Negativity' (RRN) has been observed in a number of studies with alphanumeric characters (Heil, Rauch, & Hennighausen, 1998; Heil & Rolk, 2002), letter-like shapes (Núñez-Peña, Aznar, Linares, Corral &Escera, 2005) and hands stimuli (Thayer & Johnson, 2006). It has been suggested that the RRN component is a specific correlate of MR processing (Heil, 2002). For example, the RRN is elicited during characters classification tasks in which MR processing is required but not in those that could be solved without MR (Heil, Bajric, Rösler &

Hennighausen, 1996; Heil, Rauch & Hennighausen, 1998). The observation that in MR tasks the RRN is elicited by stimuli with small rotation angles (although its amplitude is strongly reduced as compared to larger rotation angles) is consistent with the hypothesis that MR can occur even with familiar stimuli such as characters.

Despite the increasing number of studies supporting individual differences in MR between higher and lower VVI individuals (defined by VVIQ2 scores), no study to date has compared ERPs measured in these groups during a MR task. To assess whether individual difference in visual imagery vividness is associated with differences in the electrophysiological correlate of MR, participants were grouped as higher and lower VVI individuals based on VVIQ2 scores and assessed with a standard letter rotation task (e.g., Hamm, Johnson & Corballis, 2004; Heil, 2002).

In a previous ERP study, differences between low-and high-accuracy individuals in a MR task were observed by Beste, Heil and Konrad (2010) reporting larger RRN amplitudes for low accuracy individuals as compared to high performers. Accordingly, if individuals with lower VVI perform worse than those with higher VVI in the letter rotation task, a larger RRN amplitude is expected. However, given the rotation of characters is a simple task and that some studies have failed to observe a behavioural difference between higher and lower VVI groups (e.g. Logie et al., 2011), differences in accuracy rate might be subtle. It is possible that lower VVI individuals spend longer time as compared to higher VVI individuals in MR processing which might be reflected by longer RTs and prolonged duration of RRN.

2.2.2 Method

2.2.2.1 Participants

Forty-one students from University of Edinburgh were recruited for this study. All participants were right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained from each participant. Three participants were excluded from data analysis because of excessive noise in the EEG data. The resulting sample consisted of thirty-eight participants (19 males) with a mean age of 20.1 years old (range between 18 and 22 years old). All these participants were assessed with the VVIQ2 (Marks, 1999; see Appendix A for detail) and their VVIQ2 score was normally distributed (Shapiro-Wilk test: $p = .77$). Considering that the lowest VVIQ2 score in this sample is 106, relative higher and lower VVI individuals were classified by the median split of their VVIQ2 scores (Marks, 1999). This method has been used in previous studies on MR (e.g., Shen, Tsai, & Lee, 2015). Two individuals with exactly median scores were excluded. In total, eighteen higher (nine males; VVIQ2 $= 115.9 \pm 8.2$) and eighteen lower VVI individuals (nine males; VVIQ2 $= 141.3 \pm 8.2$) were grouped for data analyses. Participants were also assessed with Corsi block test (Kessels, van den Berg, Ruis & Brands, 2008). There was no significant difference between each imagery ability groups (t (34) = 1.23, p = .12). Therefore, we did not take the corsi block score into account in the data analyses.

2.2.2.2 Stimuli and procedure

On each trial, one of the upper character letters F, L, P and R was presented in their canonical way (normal letters) or vertical meridian (mirror image) at either 0°, 30°, 60°, 90°, 120° and 150° clockwise or counter-clockwise from the vertical upright position of the stimuli. The letters presented in white on a black background and had a height of 3 cm, subtending 2.26° of visual angle. Participants were seated in an electrically shielded, dimly lit, sound attenuating room. The computer monitor was located at a distance of 76cm in front of the participants, whose eyes were aligned with the monitor centre.

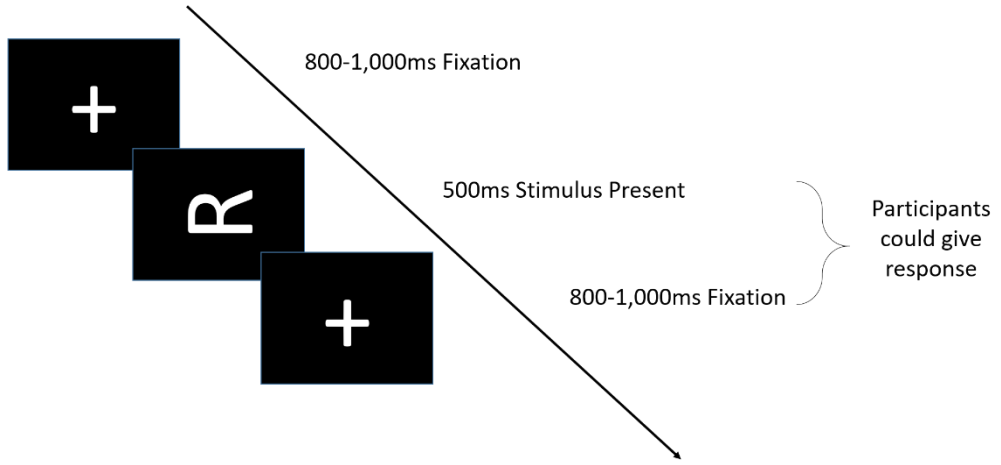

Figure 2-6. The experimental procedure in Experiment 2, 3, 7 & 8.

As depicted in Figure 2-6, each trial began with the presentation of a white fixation cross (1cm × 1cm) in the centre of a black background. One hundred milliseconds later, a letter was presented in the centre of the screen for 500ms, after which a fixation cross remained on the screen for randomly varying intervals of 1,800 - 2,100ms. Participants were instructed to respond as fast and as accurately as possible to determine whether the letter on the screen was presented a normal or mirrored

version. Letters were presented in blocks of 96 trials each. Each combination of four letters, two stimulus types, six rotation angles and two orientation of the rotation resulting in 960 experimental trials.

2.2.2.3 Electrophysiological recording

During EEG recording, participants were instructed to keep their eyes on the fixation presented on the screen and their index fingers on the two keys on the response box, which was vertically arranged in front of them. The top button was set for responses to normal stimuli and the bottom was set for responses to mirror stimuli. While the stimulus to response key mapping was held constant throughout the experiment, the responding hand to response key mapping (left hand on the top key and right hand on the bottom key) was changed after each block. To familiarize participants with the task, 48 unrecorded practice trials were added with letters “G” and “J” which were not included in the set of experimental stimuli.

EEG were acquired continuously 70 active electrodes (BioSemi Active Two system) at a sampling rate of 512 Hz, with an amplifier band pass set from 0.53 to 40 Hz. The horizontal EOG (hEOG) was monitored via a pair of tin electrodes placed at the outer ocular canthi and the vertical EOG (vEOG) was recorded via a separate bipolar montage placed at the suborbital and supraorbital ridges of the right eye. The impedances of the earlobe reference electrodes were kept as equal as possible. The EEG, hEOG and vEOG were segmented into discrete, single-trial epochs of 850ms starting at 100ms before the onset of the test stimulus. Trials with eye blinks (VEOG

exceeding ± 60 μV), horizontal eye movements (HEOG exceeding ± 80 μV) were rejected. EEG epochs containing amplitudes exceeding ± 70 μV throughout the epoch were excluded from analysis.

To further test the role of VVI in MR tasks, the correlation between the MR performance measures (averaged accuracy and averaged corrected RTs) and individual's VVIQ-2 score were tested.

2.2.2.4 Electrophysiological Data Analysis

Single trials with correct response were stored and averaged according to stimulus type (normal, mirror), rotation angle (0°, 30°, 60°, 90°, 120°, 150°) in the selected recoding sites at central-parietal lobe (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4). The data from the same rotation angle clockwise and counter-clockwise were combined. To fully assess the rotation effect on the ERP waveforms, we analysed the difference waves by subtracting the ERP waveforms associated with the upright position trials (at 0°) from the ERP waveforms elicited on different rotation angles trials (30°, 60°, 90°, 120°, 150°) in the corresponding conditions. Grand-averages of these difference waves were analysed in two consecutive measurement windows between 350 and 500ms and between 500 and 650ms respectively with General Linear Model (GLM) mixed ANOVAs with imagery ability (higher or lower VVI) as between-subject factor

as well as stimulus type (normal or mirror) and rotation angle (30°, 60°, 90°, 120°, 150°) as within-subject factors[1].

The main effect of rotation angle was further assessed by polynomial contrasts. Post-hoc analyses with further ANOVAs and trend analyses were done to further investigate significant interactions associating with rotation angle to assess the presence and characteristic of rotation angle under different rotation angles or for different imagery ability individuals. The slopes of function relating RRN amplitude to rotation angles were calculated and compared under each experimental conditions when necessary and independent t-tests (two-tailed) were done to further investigate the imagery ability effect on each rotation angle. Bonferroni correction was applied if appropriate. Greenhouse-Geisser correction was used in case of sphericity violations. Partial η^2-values for each significant main effects or interactions were reported as well as the corrected p-values.

2.2.2.5 Onset and Offset of RRN analyses

To test whether imagery abilities were associated with differences in the timing of the RRN component, the onset and offset of RRN were directly compared between higher and lower VVI individuals for both normal and mirror conditions. The

1 In the preliminary data analyses, hemisphere was taken into account with left- and right-central-parietal sits (pooled over Cp1, Cp3, P1, P3, and Cp2, Cp4, P2, P4 respectively). However, no difference involving imagery ability × hemisphere was observed in both time windows, all p-values > .05. Thus, the factor hemisphere was not included in the final analyses.

maximum RRN difference waves was computed by subtracting the ERPs elicited by the 0° condition from the waveform elicited by the 150° condition. The jackknife-based method proposed by Miller, Patterson and Ulrich (1998) applied to assess differences in onset/offset of RRN for good and poor images in the normal and mirror conditions. Jackknife approach has been demonstrated to increase the power in the analysis of ERP component onset/offset while controlling the Type I error rate (Miller et al., 1998; Ulrich and Miller, 2001; Kiesel et al., 2008) by estimating onset/offset latencies from grand averages that are computed from subsamples of participants where one participant is successively excluded from the original sample (Miller et al., 1998). This approach has been used for RRN component to compare difference between two stimulus versions (Hamm, Johnson & Corballis, 2004) or between differential experimental conditions (Heil & Rolke, 2002). Following the procedure introduced by Heil and Rolke did (2002), RRN onset/offset were computed within a 300-750ms post-stimuli time window, and were correspond to 50% of its maximum amplitude before and after the peak for each imagery ability group under different stimulus types.

Mixed ANOVAs were applied on RRN onset and offset with stimulus type (normal or mirror) as a within-subject factor and imagery ability (higher or lower VVI individuals) as a between-subject factor with correction suggested for Jackknife-based scoring in factorial design (Ulrich & Miller, 2001). Independent t-tests were done to

further investigate the imagery ability effect in each stimulus type. These planned comparisons were testing directional hypotheses, so that these tests were one-tailed.

2.2.2.6 Behavioural Data Analysis

Trials with different orientations (clockwise and counter-clockwise) were combined for each rotation angle and each stimulus type for analyses. RTs exceeding two standard deviations above or below the mean calculated separately for each participant under each experimental condition were excluded (4.6% of the trials on average). Mixed ANOVAs (GLM) were conducted with imagery ability (higher or lower VVI individuals) as a between-subject factor and rotation angles (0°, 30°, 60°, 90°, 120°, 150°) and stimulus type (normal or mirror) as within-subject factors[2]. Main effects and interactions involving the factor rotation angle were further assessed by trend analysis. Whenever a linear trend was observed for rotation angle, the slope and intercept were calculated and compared between different experimental conditions or between different imagery groups, as appropriate.

2.2.3 Results

2.2.3.1 Behavioural Results

2 Median-split RTs was done for each participants under different experimental conditions in the preliminary analyses. The speed of response (fast-, slow-response) was taken as a with-in subject factor for mixed ANOVAs, confirming a longer RTs in slow- than fast-response, $F(1, 34) = 441.275$, $p < .001$, including stimulus version $\times$ speed, rotation angle $\times$ speed, and rotation angle $\times$ stimulus type $\times$ speed interactions (all Fs ≥ 2.96, $p \leq .025$, $\eta^2 \geq .08$. However, speed was not found interacted with imagery ability, all Fs $\leq .08$, ps $\geq .78$. Therefore, the factor speed was excluded in the final analysis.

Response Times

A main effect of stimulus type was reliably present on RTs, F (1, 34) = 73.01, $p < .001$, $\eta^2 = .68$, revealing that longer RTs were required in rotating mirror (M = 601.62ms, SE = 16.54) than normal letters (M = 671.67ms, SE = 18.88).

The main effect of rotation angle on RTs was also significant (F (1.4, 48.4) = 170.39, $p < .001$, $\eta^2 = .83$) and was described by a linear (F (1, 34) = 216.02, $p < .001$, $\eta^2 = .86$) and quadratic (F (1, 34) = 68.28, $p < .001$, $\eta^2 = .67$) trend. RTs associated with each two consecutive rotation angles differed significantly from each other (all ps $< .001$). In addition, a significant rotation angle × stimulus type interaction was present, F (2.7, 90.69) = 5.05, $p = .004$, $\eta^2 = .13$. Follow-up analyses were conducted separately for each stimulus type. In the normal condition, the main effect of rotation angle, F (1.5, 52.6) = 253.23, $p < .001$, $\eta^2 = .88$, was described by a linear (F (1, 34) = 324.75, $p < .001$, $\eta^2 = .91$), quadratic (F (1, 34) = 117.52, $p < .001$, $\eta^2 = .78$) and cubic trends (F (1, 34) = 12.49, $p = .001$, $\eta^2 = .27$). Significant differences in RTs emerged in any two consecutive angles (all ps $\leq .003$). In the mirror condition, the main effect of rotation angle was present, F (1.7, 56.4) = 91.38, $p < .001$, $\eta^2 = .73$, and could be described by a linear (F (1, 34) = 130.56, $p < .001$, $\eta^2 = .79$) and a quadratic trend (F (1, 34) = 23.8, $p < .001$, $\eta^2 = .41$).

The rate of MR was slower for mirror (M = 1.45ms/degree; SE = .13) than normal stimuli (M = 1.61ms/degree, SE = .9), as revealed by the analysis of the

slopes estimated from the regression line over rotation angle (F (1, 35) = 5.55, p = .024, η^2 = .14). In addition, a larger intercept was observed for normal (M = 480.52ms, SE = 12.1) than for mirror letters (M = 563.18ms, SE = 15.0), F (1, 35) = 76.74, $p < .001$, η^2 = .69.

Although lower VVI individuals (M = 662.43ms, SE = 24.4) were numerically slower than higher VVI individuals (M = 610.86ms, SE = 24.4) no main effect of imagery ability was present in the RT analysis, F (1, 34) = 2.23, p = .145. No other interactions involving imagery ability emerged to be significant (all Fs (1.4, 48.5) $\leq$ 1.61, all ps $>$ .159).

Accuracy

A main effect of stimulus type emerged to be significant, F (1, 34) = 4.79, p = .036, η^2 = .12, revealing higher accuracy rates for mirror (M = 94.5%, SE = 1.0) than normal letters (M = 93.3%, SE = .9). The analysis on accuracy rates also yielded a significant main effect of rotation angle, F (1.8, 61.9) = 34.1, $p < .001$, η^2 = .50. Accuracy rates dropped significantly from 93.5% (SE = 1.0) at 120° to 87.0% (SE = 1.8) at 150°, $p < .001$, and from 94.8% (SE = .7) at 90° to 93.5% (SE = 1.0) at 120°, p = .050. Accuracy rates gradually decreased with increasing rotation angles, as suggested by a linear (F (1, 34) = 45.44, $p < .001$, η^2 = .57), a quadratic (F (1, 34) = 28.86, $p < .001$, η^2 = .46) and a cubic trend (F (1, 34) = 14.97, $p < .001$, η^2 = .306). In addition, rotation angles interacted with stimulus type, F (1.3, 44) = 9.45, p = .002, η^2 = .22. In the normal condition, a main effect of rotation angle , F (1.3,

43.7) = 27.76, $p < .001$, $\eta^2 = .45$, revealed that the accuracy decreased with increasing rotation angles as described by linear (F (1, 34) = 29.48, $p < .001$, $\eta^2 = .46$), quadratic (F (1, 34) = 30.34, $p < .001$, $\eta^2 = .47$) as well as cubic trends (F (1, 34) = 14.92, $p < .001$, $\eta^2 = .31$). Responses to 150°-rotated normal letters (M = 81.5%, SE = 2.9) were less accurate than those to 120°-rotated stimuli (M = 91.8%, SE = 1.6), $p < .001$. However, no main effect of rotation angle emerged in the mirror letter rotation tasks, F (1.6, 54.8) = 1.35, $p = .246$.

No statistical difference emerged between accuracy rates of lower (M = 93.3%, SE = 1.3) and higher VVI individuals (M = 94.5%, SE = 1.3), F (1, 34) = .42, $p = .522$. In addition, no interactions involving imagery ability-related were observed on the accuracy rates (all Fs (1.3, 44) $\leq$ .95, all ps $\geq$ .36).

Correlations

The VVIQ-2 score did not show significant correlation with either RTs, (r = -.14, p = .41) or accuracy rate (r = -.18, p = .30).

2.2.3.2 Electrophysiological data

Figure 2-6a shows the grand-averaged waveforms representing the RRN component observed in higher and lower VVI individuals (top and bottom panels, respectively) during the mental rotation of normal and mirror letters (left and right panels, respectively). These waveforms pooled over central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) and calculated by subtracting ERPs in upright position (0°) from each of the rotation angles (30°, 60°, 90°, 120° and 150°) from 0°. Figure 2-6b shows

the corresponding mean amplitude values calculated for higher and lower VVI individuals in trials with normal and mirror letters separately in the late RRN time window (500-650ms). A summary of the rotation angle effects in this interval (500-650ms) for higher and lower VVI individuals is presented in Table 3-1 separately for normal and mirror letter trials.

A reliable rotation angle main effect was present in both time windows measured between 350-500ms (F (2.7, 92.6) $= 37.44$, $p < .001$, $\eta^2 = .52$) and 500-650ms (F (2.3, 77.4) $= 24.13$, $p < .001$, $\eta^2 = .42$). As shown in Figure 2-6a, RRN amplitudes became more negative with the increasing rotation angles in both time windows and were confirmed fit for a linear trend only (350-500ms: F (1, 34) $= 71.25$, $p < .001$; 500-650ms: F (1, 34) $= 12.41$, $p < .001$, $\eta^2 = .27$). Further post-hoc analyses carried out and revealed that MR effort was reliably present in smaller rotation angles (30°-60°: $p < .001$; 60°-90°: $p = .004$) in the early RRN time windows (350-500ms), whereas such effort was evident in larger rotation angles (90°-120°: $p = .010$, 120°-150°: $p < .001$) in the late RRN time windows (500- 650ms).

There was no main effect of stimulus type observed between 350 and 500ms post-stimuli, F (1, 34) $= .54$, $p = .469$. However, the interaction of rotation angle and stimulus type emerged to be significant in this interval, F (4, 136) $= 14.61$, $p < .001$, $\eta^2 = .30$. The main effects of rotation angle were present for both normal (F (3.2, 109.5) $= 46.63$, $p < .001$, $\eta^2 = .58$) and mirror stimuli (F (2.9, 97.5) $= 7.11$, $p < .001$, $\eta^2 = .17$). In the normal condition, significant RRN amplitude differences

were found in the following two consecutive angles: 30°-60° ($p = .008$), 60°-90° ($p = .009$) and 90°-120° ($p = .012$). In the mirror condition, such RRN difference was only presence between 30° and 60° ($p = .030$). In both cases, RRN amplitudes became more negative with increasing rotation angles and fit for a linear trend (normal: F (1, 34)=115.85, $p < .001$, $\eta^2 = .77$; mirror: F (1, 34) = 12.41, $p = .001$, $\eta^2 = .27$). The subsequent slope analysis on RRN mean amplitude of rotation angles yielded a more pronounced RRN in the normal (M = -.023μV/degree, SE = .002; see Figure 2-6a, left panel) than mirror condition in this interval (M = -0.008μV/degree, SE = .002; Figure 2-6a, right panel), F (1, 34) = 44.84, $p < .001$, $\eta^2 = .57$.

In the time window measured between 500 and 650ms, a main effect of stimulus type reliably present, F (1, 34) = 43.31, $p < .001$, $\eta^2 = .56$, revealing a larger RRN amplitude observed in the mirror (M = 1.36μV, SE = .17) condition as compared to that in the normal one (M = -.20μV, SE = .24). Stimulus type was not found interacted with rotation in this interval, F (2.8, 94) = 2.57, $p = .064$.

No main effect of imagery ability or related interactions emerged in the early RRN time window (350-500m). By contrast, differences between imagery abilities groups emerged in the late RRN interval (500-650ms), F (1, 34) = 4.33, $p = .045$, $\eta^2 = .11$, revealing larger RRN amplitudes in lower (M = .93μV, SE = .24) than in higher VVI individuals (M = .23μV, SE = .24).

Moreover, a three-ways interaction between imagery ability, stimulus type and rotation angle was present between 500 and 650ms, F (2.8, 94) $=$ 3.53, $p = .021$, $\eta^2 = .09$. Follow up analyses were conducted separately for the different stimulus types. The group $\times$ rotation angle interaction emerged to be significant in the normal letter condition (Figure 2-6a, left panel), F (2.5, 84.9) $=$ 3.7, $p = .021$, $\eta^2 = .10$. The main effect of rotation angle in higher VVI individuals, F (2.2, 37.1) $=$ 3.35, $p = .042$, $\eta^2 = .16$, revealed that RRN amplitudes were significantly larger at 150° as compared to 120° ($p = .029$), whereas no difference emerged between any other two consecutive rotation angles, all ps $\geq .58$. Trend analyses confirmed that the RRN amplitudes were fit for quadratic trend only in these individuals with higher VVI (see Table 2.1). A main effect of rotation angle was also evident in lower VVI individuals, F (2.7, 45.79) $=$ 16.08, $p < .001$, $\eta^2 = .49$. The RRN amplitude increased with the increasing rotation angle and as revealed by trend analyses fit for both a linear and a quadratic trend in lower VVI individuals (see Table 2.1). The RRN amplitudes were significantly larger at 150° as compared to 120° ($p = .019$) and the difference between 90° and 120° approached significance ($p = .064$). In the mirror condition, there was no interaction between group and rotation angle, F (2.3, 78.3) $=$ .86, $p = .44$. However, to characterize the higher and lower VVI individuals' mirror letter rotation performances in this late RRN time window, further analyses conducted in each imagery ability group. The presence of rotation angle main effects in both higher (F (2.3, 38.2) $=$ 13.66, $p < .001$, $\eta^2 = .45$) and lower VVI individuals (F (2.1, 36.2) $=$ 6.3, $p = .004$,

$\eta^2 = .27$) revealing the fact that the RRN amplitudes became more negative with increasing rotation angles. As shown in Table 1, RRN amplitudes fit for both a linear and a quadratic trend for higher VVI individuals, but were linearly correlated with rotation angle only in lower VVI individuals.

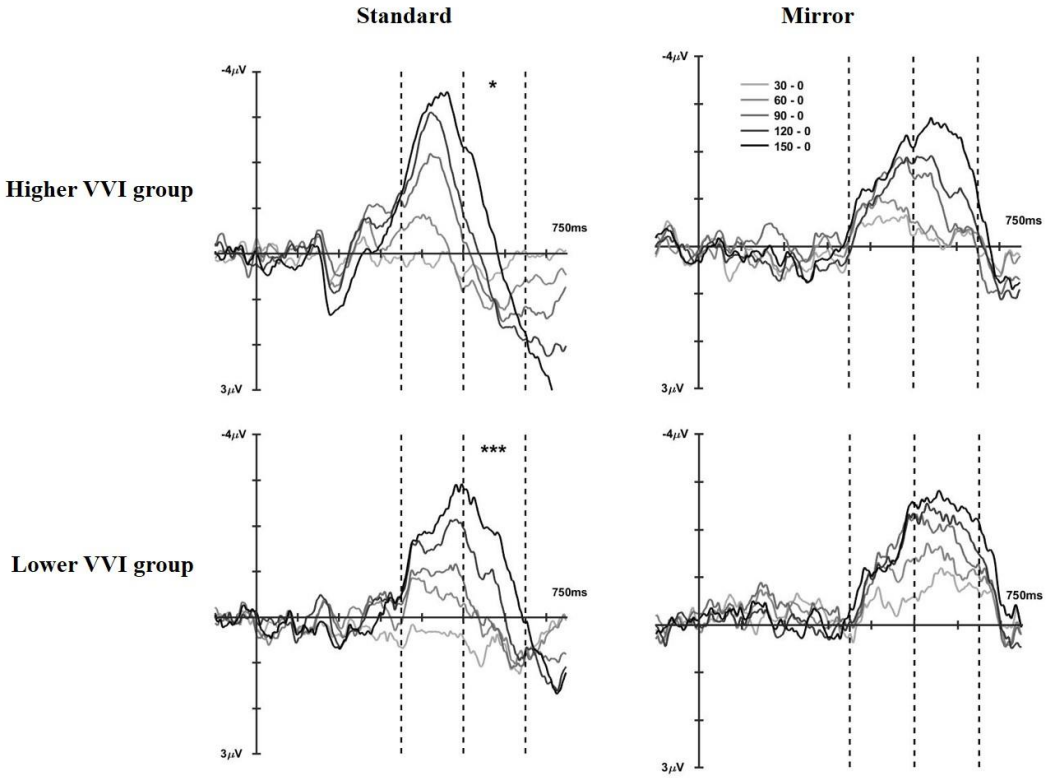

Figure 2-7. Brain potential performances in normal and mirror letter rotation for higher and lower VVI individuals (n = 18 respectively). Figure 2-6a shows grand-average rotation-related negativity (RRN) calculated by subtracting ERP waveforms elicited on the non-rotation trials (0°) from ERPs elicited on different rotation angles trials (30°, 60°, 90°, 120°, 150°) at central-parietal sites (CPz, CP1/2, CP3/4, Pz, P1/2, P3/4) elicited by normal (left panel) and mirror letters (right panel) and separately for higher (top panel) and lower VVI individuals (bottom panel).

Table 2.1 *The percentage of the variance explained by significant linear and quadratic trend components for higher and lower VVI individuals in each stimulus type.*

Imagery Group	Trend Components	Normal	Mirror
Higher VVI group	Linear	n.a.	60% F (1, 17) = 25.7, $p < .001$
	Quadratic	44% F (1, 17) = 13.48, $p = .002$	22% F (1, 17) = 4.8, $p = .043$
Lower VVI group	Linear	65% F (1, 17) = 31.74, $p < .001$	37% F (1, 17) = 9.84, $p = .006$
	Quadratic	22% F (1, 17) = 4.78, $p = .043$	n.a.

2.2.3.3 Onset and Offset of RRN

Figure 2-7 shows the time course of the RRN differences waves for higher (black solid line) and lower VVI individuals (grey dotted line). The RRN difference waves obtained by subtracting ERPs elicited at 150° from ERPs at upright position (0°) pooled over central-parietal sites (CPz, CP1/2, CP3/4, Pz, P1/2, P3/4). A prolonged MR process is visible in lower as compared to higher VVI individuals with RRN component diminished later on trials elicited in lower relative to trials elicited in higher VVI individuals.

Onset of RRN

A main effect of stimulus type emerged, $F_c\,(1, 34) = 5.75$, $p_c = .01$, revealing the fact that the occurrence of the pure MR process starts later in the mirror condition (M = 438.65ms, SE = 1.69) as compared to normal letters processing (M = 368.61ms, SE = .37).

The imagery ability main effect did not reached the significant level ($F_c\,(1, 34) = .97$, $p_c = .17$) on the onset of RRN. No group × stimulus type interaction ($F_c\,(1, 34) = .13$, $p_c = .36$) was found on the onset of RRN.

Offset of RRN

The analyses on RRN offset revealed a main effect of stimulus type, $F_c\,(1, 34) = 50.73$, $p_c < .001$. The offset of RRN was delayed in processing mirror letters (M = 662.23ms, SE = .82) as compared normal ones (M = 563.16ms, SE = .5).

A main effect of imagery ability was reliably observed on the RRN offset ($F_c\,(1, 34) = 7.6$, $p_c = .004$). As shown in Figure 2-7, higher VVI individuals had completed their MR processing at around 587.3ms (SE = .77), while lower VVI individuals were still rotating until around 638.08ms (SE = .77). However, imagery ability was not found to interact with stimulus type, $F_c\,(1, 34) = .74$, $p_c = .2$.

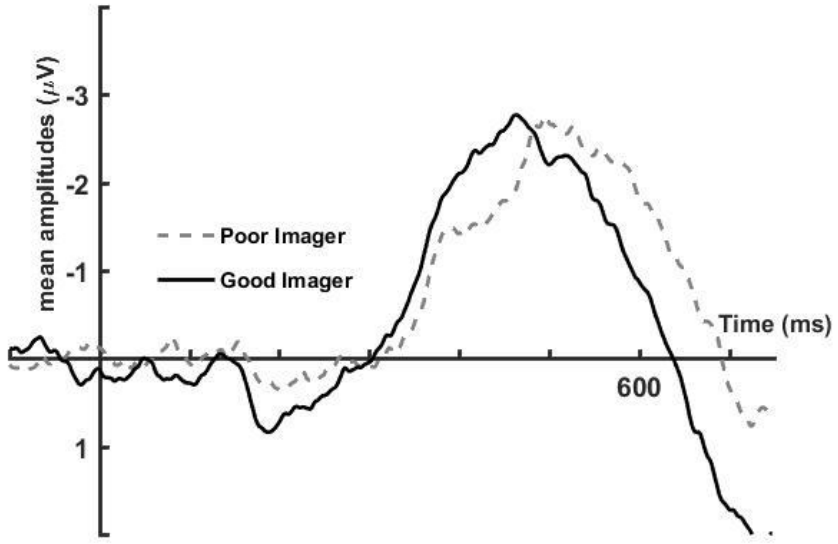

Figure 2-8. Rotation-related negativity (RRN) difference waves obtained by subtracting ERPs elicited at 0° trials from ERPs elicited at 150° at central-parietal sites (CPz, CP1/2, CP3/4, Pz, P1/2, P3/4) separately for higher (black solid line) and lower VVI individuals (grey dotted line).

2.2.4 Discussion

In the present study, higher and lower VVI individuals (defined as individuals with low and high level of visual imagery vividness) were assessed with a standard letter MR task to investigate whether differences in visual imagery vividness are reflected by differences in the electrophysiological correlate of MR, the RRN. This ERP component was obtained by subtracting the ERP waveforms elicited in the upright position (0°) from those elicited in each rotation angle (30°, 60°, 90°, 120°, 150°) separately for each participant and each stimulus type.

Results replicated the classic effect of rotation angle on both behavioural (Shepard & Metzler, 1971) and ERP measures (Hamm et al., 2004; Heil & Rolke, 2002; see Heil, 2002, for review). RTs linearly increased with increasing rotation angles and RRN amplitudes (measured between 350 and 650 ms post stimulus) became more negative with increasing rotation angle.

Crucially, we observed systematic RRN differences between higher and lower VVI individuals. More specifically, we observed a longer duration of the pure MR process in lower imagers as compared to higher VVI individuals, as revealed by the fact that the onset of the RRN component was similar across groups but its offset was delayed in lower VVI individuals. This difference in the time course of the RRN was also reflected in the analysis of mean RRN amplitudes. While no difference between imagery groups was present in the initial RRN time window (350- 500ms), larger RRN amplitudes were observed for lower than higher VVI individuals.

This RRN amplitude difference between groups is in line with the findings of a recent ERP study in which participants were grouped into low- and high-performers based on the median split of their accuracy performance (Beste, Heil and Konrad, 2018). Larger RRN amplitudes were observed across angles for low- as compared to high-performers, suggesting that low-performers had to increase their MR effort to cope with the MR task (i.e., the neural efficiency hypothesis; Haier et al., 1988; Neubauer & Fink, 2009). However, in the present study the RRN amplitude differences between groups were present in the late but not in the early time window.

This observation, together with the systematic delays in RRN offset for lower VVI individuals, suggests that the amplitude differences between groups are more likely to be driven by a prolonged rotation process rather than an increased rotation effort in lower VVI individuals. In other words, the RRN amplitudes were reduced in higher compared to lower VVI individuals in the late RRN time window because higher VVI individuals completed MR earlier than lower VVI individuals.

This hypothesis is further supported by the finding that the RRN measured between 500 and 650ms post-stimulus during the rotation of normal letters in lower VVI individuals increased linearly with increasing rotation angles. This suggests that the MR process proper is still executed in this time window. By contrast, the RRN measured in higher VVI individuals in the different rotation angles could be described by a quadratic trend only revealing that higher VVI individuals had already completed the rotation of letters presented at small rotation angles in this late time window. It is worth noting that this group difference was observed during the rotation of normal but not mirror stimuli. Because the RRN elicited during mirror letters rotation occurs later than that elicited during normal letters (Hamm et al., 2004; Núñez-Peña, & Aznar-Casanova, 2009), it is possible that both groups were still rotating mirror stimuli in the 500-650ms post-stimulus interval. The analysis of RRN offset which is not constrained by a set time limit did not show any reliable difference between rotations of normal and mirror letters, suggesting similar delays across stimulus types.

Taken together, the findings of the present study suggest that the MR process was prolonged in lower relative to higher VVI individuals. In which way the different duration of MR process in higher and lower VVI individuals can be related to their ability to create and maintain the mental representations? The precision of the visual representation is correlated with the speed of MR: more precise visual representations were shown to be associated with a faster execution of the MR process (e.g. Mumaw et al., 1984). MR rate is also modulated by the amount of information stored in mental representation. Recent evidence has shown that the MR process is slower when the visual representations are more detailed and contain more information (Liesefeld & Zimmer, 2013; Liesefeld et al., 2015).

The content (amount of information extracted) and accuracy of the visual representation varies across individuals (Liesefeld et al., 2015; Marks, 1973; see Reeder, 2017 for a review). Higher VVI individuals are capable to create and maintain more accurate visual representations (Marks, 1973) and might therefore be able to complete the MR process faster than those with higher VVI. By contrast lower VVI individuals which are more likely to create less accurate mental representations, may encode additional but unnecessary information which might extend the rotation process.

This possibility could be further speculated referring to neural efficiency in terms of different strategy selection by higher and lower VVI individuals. According to neural efficiency hypothesis (Haier et al., 1988; Neubauer & Fink, 2009), a more

efficient human nervous system could also result in a less consuming time as indexed by a temporally negative association between ERP component and cognitive abilities (Deary, 2000; Deary and Caryl, 1997). Therefore, individuals with lower VVI in the current study are probably less efficiency in the MR proper and therefore finished their MR processing later as relative to those with higher VVI. Higher VVI individuals who maintained a simplified internal representation, possibly adopted holistic strategy throughout the MR task in the current study. For lower VVI individuals, the less precise mental representation may restrict their holistic strategy usage and piecemeal transformation has to be applied instead. This case may vary depends on the task demand (i.e. the extent to be rotated). For example, individuals with lower VVI may apply holistic for some easy trials (i.e. smaller rotation angles) where the accurate internal representation can maintain during MR execution and use piecemeal transformation for other more difficult trials (i.e. larger rotation angles) with less accurate representation in their minds. That is to say, lower VVI individuals may apply different strategies to cope with this letter rotation task and they may change their strategies depending on the tasks demand from trial-to-trial.

This possibility provides a reasonable explanation to account why there is an imagery ability difference in MR execution as indexed by RRN component, but did not show such discrepancy in RTs performance. RTs measurement reflects a combined contribution of multiple, interacting stages of neural processing. According to the traditional theories of mental rotation (e.g., Corballis, 1988; Shepard & Cooper, 1982),

functional independent information sub-process can be differentiated. Once the MR execution is finished, higher VVI individuals who more stick to holistic strategy have to judge the parity of the stimuli before a response is given. On the other hand, individuals with lower VVI who vary with their strategy selections and more likely to rely on piecemeal transformation may judge the stimuli parity after each mental transformation. In this case, the parity judgment sub-process and MR proper may temporally overlapped, as observed in some others (e.g., Schendan & Lucia, 2009). Hence, less time is required in lower as compared to higher VVI individuals in the sub-process between MR processing is finished and before a response is executed. However, it is notable that no direct evidence in the present experiment could support the idea that different strategies were chosen by individuals. Future studies could be conducted to verify this speculation.

Despite fact that ERP results consistently suggested an extended rotation process for lower as compared to higher VVI individuals, this difference was not present in the behavioural measures (RTs or accuracy rate). It is possible that the letter rotation task used here is too easy to elicit consistent differences in performance between groups. It is also possible that the prolonged duration of MR process proper in lower VVI individuals was compensated by a reduced duration of subsequent cognitive processes, resulting in no imagery ability discrepancies in the behavioural measures which reflect the end result of different cognitive processes. In this context it is worth noting that in line with existing evidence (Logie et al., 2011) brain imaging

methods can highlight subtle individual differences between higher and lower VVI individuals that would not be evident with behavioural measures alone.

2.3 Experiment 3

2.3.1 Introduction and brief recap

Despite behavioural and ERPs evidence have shown differential MR performances across individuals with different levels of visual imagery ability in the first two experiments, there is no direct evidence so far to test the functional role of visual imagery in MR tasks.

One way to investigate the functional role of visual imagery in MR is to examine individuals who no longer have visual experiences. Some philosophic arguments (Drever, 1955) and later some experimental data allowed the authors to claim that blind people, still have the ability to generate visual representations (Kerr, 1983; Cornoldi, Cortesi, Preti, 1991; Cornoldi, & Vecchi, 2003). MR performance was tested among early blind, late blind and sighted individuals (Marmor & Zaback, 1976). Although sighted individuals performed generally faster than blind people, the typical linear RTs were observed in all groups of participants suggesting that visual experience as such is not necessary in performing a MR task. However, it has been suggested that haptic experience could take over from visual experience in generating visual representations in one's mind (Hollins, 1985). Such visual representations are not the same as those experienced by sighed people, because the structure of mental imagery seems to change progressively after the loss of sight.

Besides blind people, some other individuals who reported a lack of visual imagination are reported in the literature (Faw, 2009; Zeman, Dewar, Della Sala, 2015).

Zeman et al. (2010) documented the case of M.X., who subjectively reported the loss of his ability in generating images in his mind and showed poor vividness in visual imagery. He performed normally on a wide range of mental imagery tasks and other cognitive tasks, except on a MR task with the typical arm-like cube as stimuli (Shepard & Metzler, 1971). He was accurate in this task but showed a non-linear pattern in RTs of rotation angle. According to his debrief, he attempted to match individual cubes and angles perceptually before responding, using a strategy not involving MR processing (Zeman et al., 2010). However, behavioural measures can only provide indirect evidence about the cognitive processes engaged during MR tasks.

Therefore, in the present study, we aimed to ascertain whether MR tasks could be complied with in the absence of depictive mental representations. More specifically, in the current study we focused on two issues: 1) whether MR task could be completed by alternative strategy instead of the execution of MR proper; and 2) whether a non-depictive format of representation could be generated and adopted in MR tasks. To this end, M.X., was tested with letter rotation tasks for normal and mirror stimuli in a ERPs study. The presence of the RRN elicited on normal and mirror letter trials would be considered an indicator for the pure process of MR. As letters are highly accessible and encountered in everyday activities, we hypothesized that a non-depictive mental representation (e.g., language-like) might be generated for normal letters by M.X and MR processing would still be adopted in this condition where the typical behavioural and psychophysiological index would still be present. In contrast, it would be relatively

difficult to generate an alternative format for mirror-version letters. According to previous observations (Zeman et al., 2010), we hypothesized that M.X. would use a different strategy that does not rely on the mental representation to comply with the MR tasks with mirror letters, rather than the typical process of MR. If this is the case, no RRN would be detected in M.X. whereas M.X. could still perform as well as controls, as he did in Zeman et al.'s study (2010).

2.3.2 Method

2.3.1.1 Participants

M.X. is a 71-year-old retired surveyor, who reported a sudden loss of his visual imagery ability after underging coronary angioplasty (remodelling of coronary arteries performed from within the arteries). Zeman et al. documented him as a case of 'blind imagination' (2010). Twelve controls were also recruited in the present letter rotation task. One was excluded for analysis due to his low accuracy in both conditions. The control participants were matched for age (mean = 70.8, range 65-76 years old), handedness (right-handed), sex (male), IQ and education (13-15 years) with M.X. We administered three standard tests: (1) IQ: Wechsler adult intelligence scale-III (Wechsler, 1997); (2) subjective vividness of visual imagery: vividness of visual imagery questionnaire (VVIQ-2; Marks, 1995); (3) visuospatial working memory: Corsi block task (Kessels, van den Berg, Ruis & Brands, 2008).

All controls had no history of neurological or psychiatric disorders, had normal or corrected normal vision and all gave informed consent to participate in the study.

2.3.1.2 Stimuli and procedure

Stimuli and experiment procedure (see Figure 2-6) were identical in Experiment.2.

2.3.1.3 EEG Recoding and pre-processing

The EEG recording and pre-processing was also identical in Experiment.2.

3.4.1.4 Data analysis

For each rotation angle, the data from clockwise and counter-clockwise were combined for both the behavioural and ERP data analysis. To test whether M.X. will show deficit in this letter rotation task, the accuracy rates collapsed across all rotation angles (0°, 30°, 60°, 90°, 120° and 150°) were first analysed for normal and mirror letters separately. The procedure developed by Crawford and Garthwaite (2002; see also Crawford & Howell, 1998) was implemented[3] to compare the accuracy rates between M.X. and the control group, separately for normal and mirror stimuli. In contrast to the use of z-scores, the current method treats the control sample statistics as statistics rather than as parameters and compares the single subject's score to the control group's score by using a non-central t distribution.

[3] The program singlism.exe (available in http://homepages.abdn.ac.uk/j.crawford/pages/dept/SingleCaseMethodology.htm) was applied.

Following the same procedure used for accuracy rates (Crawford & Garthwaite, 2002; Craw & Howell, 1998), the comparison was conducted on RTs for letters in the upright position (0°) between M.X. and the control group for normal and mirror letters separately. As our primary interest, RTs for rotated letters (30°, 60°, 90°, 120° and 150°) were then analysed. Similar to Logie et al. did (2011), the RTs for rotated letters were corrected in order to control for the potential influence of the inter-participant difference in baseline performance (0°). That is, for each participant each rotation angle (30°, 60°, 90°, 120° and 150°) mean RTs were subtracted from those measured on no rotation trials (0°). Crawford and Garthwaite's procedure (2002) was then applied on these corrected RTs for normal and mirror trials separately to test whether M.X. performed differentially across all rotation angles as compared to the controls.

Additional analyses were conducted to further characterize the performance associated with different rotation angles in M.X. and the control group. First, Pearson correlation coefficient was computed for individual participant in trials with normal and mirror letters separately to test whether the typical increment RTs with rotation angles was present in M.X. and control group[4]. The subsequent analysis with intra-individual measures of association (IIMAs; Crawford, Garthwaite, Howell & Venneri,

[4] The RTs for each control could fit for a linear line in both standard (all p-values $\leq$ .047) and mirror condition (all *p*-values $\leq$ .043). For M.X., RTs could also fit for a linear trend in both standard ($p = .009$) and mirror condition ($p = .043$). Therefore, the estimated slope measured were computed by the linear trend analysis in each condition for further slope analysis. However, the analyses were rejected for both standard and mirror letters as at least one control's error was significantly smaller or larger other controls' error variances.

2003) was applied[5] to compare the correlation coefficient between M.X. and the control group for each stimulus type. According to this method (Crawford et al., 2003), Fisher's transformation was applied to the correlation for individual participant as Pearson's r is not normally distributed. The transformed correlation of M.X. was then compared with the mean and standard deviation of the transformed correlation in the control group using the *t*-distribution.

Mean amplitude values for the ERP analyses were quantified over central-parietal electrodes (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) as selected in Quan et al. (2017) within a predefined measurement windows 350 - 650ms post-stimulus for each participant, each stimulus type (normal vs mirror) and each rotation angle (0°, 30°, 60°, 90°, 120° and 150°). Methods of statistical analysis for ERP data were consistent with methods for behavioural data. First, ERP amplitudes for letters in the upright position (0°; baseline) were compared between M.X. and his controls in normal and mirror letters separately by applying Crawford and Garthwaite' procedure (2002; Craw & Howell, 1998). Similar to the procedure in the analysis of RTs, RRN amplitudes were calculated by subtracting ERPs elicited by letters at 30°, 60°, 90°, 120° and 150° rotation angles from those elicited by upright letters (0°) to remove the potential influence inter-participant differences in baseline performance. Cwaford and Garthwaite's procedure (2002; Craw & Howell, 1998) was applied on RRN amplitudes

[5] The program iima.exe (available in http://homepages.abdn.ac.uk/j.crawford/pages/dept/SingleCaseMethodology.htm) was applied.

collapses cross all rotation angles (30°, 60°, 90°, 120° and 150°) in normal and mirror trials separately to test whether M.X. performed differently on rotated letters.

In addition, to further characterize the MR processing and to test whether the typical MR pattern can be observed in each experimental condition, the correlation coefficient between RRN amplitudes and rotation angles was calculated for M.X. and individual control participants in normal and mirror letters separately. IIMAs (Crawford et al., 2003) was then conducted to compare the corrected correlation coefficient (after Fishers' transformation) between M.X. and the control group[6].

2.3.3 Results

The demographic variables for M.X. and for the eleven controls are summarised in Table 2.2. M.X. was well matched with control participants on general intelligence (full scale IQ 136 in M.X. vs. 139 in control participants). In VVIQ2 test (Marks, 1995), M.X. showed significant lower scores than the controls.

Table 2.2 *Demographic variables for M.X. and matched controls.*

	M.X.	**Control mean**	**Control SD**
age	71	70.6	3.1
WAIS-III	136	138.9	6.5
VVIQ2 (/160)	32*	140.4	11.2
Corsi block	4	4.6	0.7

[6] ERPs for M.X. could be fitted for a linear trend in the standard condition ($p = .007$) but not in mirror letter processing ($p = .478$). Therefore, the slope of ERP amplitudes could not be obtained for further analyse.

2.3.3.1 Behavioural data

The analysis of accuracy rates showed that M.X. (normal = 96.3%; mirror = 94.2%) performed as well as his controls (normal = 95.5% ± 3.1; mirror = 93.7% ± 3.7) during the MR of normal (t (10) = 0.24, p = 0.41) and mirror letters (t (10) = 0.13, p = 0.90). The estimated percentage of normal population performing worse than M.X. is 38.87% for normal and 32.20% for mirror letters.

The RT analysis revealed no difference between M.X. and the control group on trials with upright letters (baseline condition) for both normal (M.X. = 541.37ms, controls = 699.17ms, SE = 158.27; t (10) = -.96, p = .18) and mirror letters (M.X. = 780.36ms, controls = 784.91ms, SE = 147.09; t (10) = -.03, p = .49). For trials with rotated letters, as depicted in Figure 2-9, left panel, M.X. and control did not differ on normal letter trials (corrected RTs: MX = 135.59ms, Controls = 138.43ms, SE = 68.13), t (10) = -0.04, p = .484. However, for mirror letters M.X. (corrected RTs = 94.06ms) performed faster than his controls (corrected RTs = 197.07ms, SE = 55.76), t (10) = -1.77, p = .054 (see Figure 2-9, right panel).

Moreover, when processing normal letters (Figure 3-8, left panel) both MX and controls showed a positive association between corrected RTs and rotation angles (M.X: r = .96, p = .009; control group: r = .77, p < .001). Further IIMAs analyses on the transformed correlation coefficients (the corrected r' for M.X. = 1.97; r' for controls = 1.83 ± 0.28) revealed that there was no difference between M.X. and his

controls on normal letter trials, t (10) $=$ 0.49, p $=$ 0.32. The estimated percentage of normal population falling below M.X.'s coefficient is 44.63%.

On mirror letter trials, as shown in Figure 3-8, right panel, the positive association between corrected RTs and rotation angle was evident for both M.X. (r $=$ .96, p $=$ .009) and the control participants (r $=$ .78, p $<$ .001). IIMAs were further conducted and revealed that the transformed correlation coefficient between RTs and rotation angle measured in M.X. did not statistically differ from that of controls (the corrected r' for M.X. $=$ 1.42; r' for controls $=$ 1.72 $\pm$ 0.35; t (10) $=$ -0.82, p $=$ .22). The estimate for the normal population to show less association between RTs and rotation angle as compared to M.X is 6.22% chance.

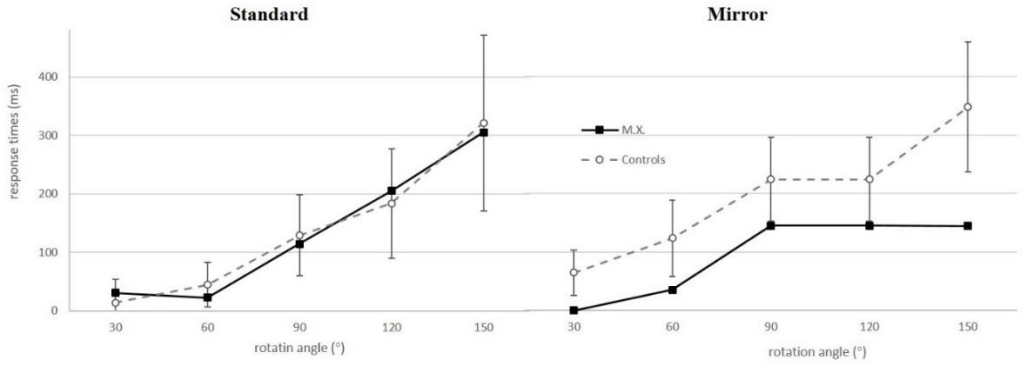

Figure 2-9. The mean relative correct response times across rotation angles for M.X. and his control group. Dashed lines represent 95% confidence interval.

2.3.3.2. Event-related potentials

For trials with letters in the upright position (0°; baseline condition), larger ERP amplitudes were observed in M.X. (normal $= 9.27\mu V$; mirror $= 12.06\mu V$) than his controls (normal $= 3.20\mu V \pm 1.6$; mirror $= 3.88\mu V \pm 2.4$) in processing either normal (t (10) $= 3.72$, $p = 0.002$) or mirror letters (t (10) $= 3.23$, $p = 0.005$).

For trials with rotated letters, there was no RRN amplitude (the ERP difference waves collapsed cross all rotated angles) between M.X. and controls in both normal (t (10) $=$ -.01, $p = .50$) and mirror condition (t (10) $= 1.40$, $p = .09$) after correcting for intra-participant baseline.

The RRN amplitudes across rotation angles were further characterized for M.X. and his controls for trials with normal and mirror letters separately by examining the correlation coefficient between rotation angles and RRN amplitudes. During the MR of normal letter, there was a significant correlation between RRN amplitudes and rotation angles in both M.X. (r $=$ -.97, $p = .007$) as well as his controls (r $=$ -.47, $p < .001$). As shown in Figure 2-10, left panel, for both M.X. and controls, RRN amplitudes became more negative with increasing rotation angles. The subsequent analyses with IIMAs confirmed that the coefficient measured in M.X. on normal letter trials (r' $=$ -2.03) was not statistically different from that observed in the control group (r' $=$ -1.09 $\pm$ 0.73), t (10) $= 1.24$, $p = 0.12$. The estimated percentage of normal population falling below M.X.' rotation coefficient in the normal condition is 67.75%.

For mirror letter trials (Figure 2-10, right panel), the control group showed a significant correlation between RRN amplitude and rotation angle (r $=$ -.47, p

$<$ .001), indicating that RRN became more negative with increasing rotation angles. However, M.X. showed little correlation between RRN amplitudes and rotation angles (r $=$ .42, p $=$ .48). The IIMAs on the transformed correlation coefficient between RRN amplitudes and rotation angles revealed a significant difference between M.X. (r' $=$ .45) and controls (r' $=$ -.83 $\pm$ 0.61) in mirror letter processing, t (10) $=$ -2.01, p $=$ 0.036. There is only 0.08% estimated chance for the normal population to show an association between RRN and rotation angle lower than M.X. on mirror letter trials.

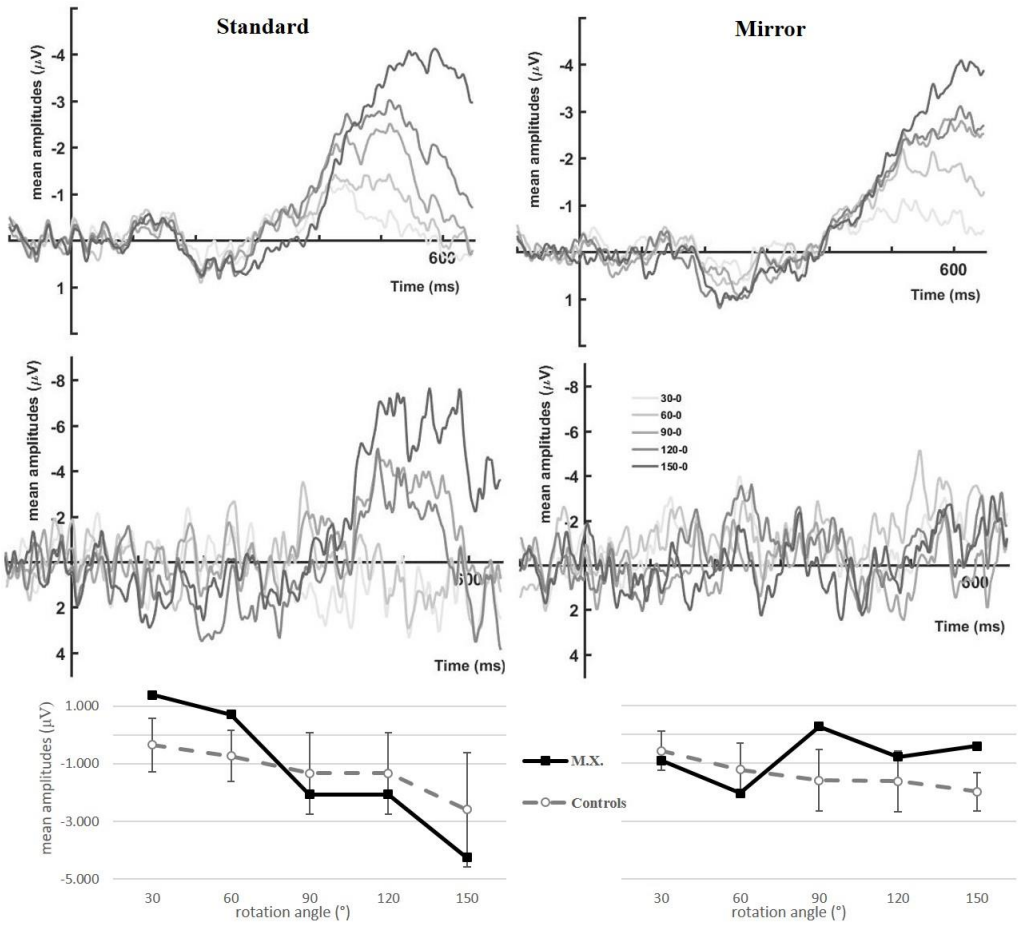

Figure 2-10. The grand-averaged difference waveforms elicited by normal and mirror letters at each rotated angles (30°-0°, 60°-0°, 90°-0°, 120°-0°, 150°-0°) pooled across central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for the control group

(N = 11; upper panel) and M.X. (the middle panel). The amplitude mean (in microvolts) in the 350-650ms time window for M.X. (black solid line) and his matched controls (grey dotted line) in processing normal and mirror letters.

2.3.4 Discussion

The present ERP study was carried out to test whether the depictive mental representation is necessary to complete MR tasks with normal and mirror letters by assessing M.X., a case of "blind imagination".

For both normal and mirror letters, M.X. successfully completed the rotation task and performed as well as control participants, replicating Zeman et al.'s findings (2010). As our primary interest, M.X. and the controls' performances (RTs and ERPs) on rotated letters were examined in detail for different stimulus type.

In the normal condition, no differential performance was observed between M.X. and controls in either RTs or ERPs. Interestingly, the specific behavioural and psychophysiological correlates of MR proper was reliably present in M.X. This finding suggests that even in the absence of visual imagery M.X was still able to mentally rotate normal letters. Pearson and Kosslyn' (2015) have recently postulated that the visual information can be stored in multiple formats, symbolic, language-like, descriptive format (i.e., propositional/non-depictive; Pylyshyn, 1981, 2003) or depictive (e.g., Kosslyn, Thompson, & Ganis, 2006; Paivio, 1971). Thus, MX might have stored the representation of the everyday encountered normal letters in an alternative format (i.e. language-like), not as an image. If this were the case, they

typical modulation of RRN amplitudes associating with rotation angle, in turn, can not only indicate the MR processing with depictive representation (Heil, 2002), but also represent the rotation process with non-depictive or abstract information consistent with Liesefeld and Zimmer's suggestion (2013). In other words, the RRN might be a general psychophysiological marker for the pure process of MR, regardless of the format of mental representations.

In processing rotated mirror letters, MX showed the high accuracy suggests that he was able to complete the MR task successfully. However, he performed differentially as compared to the controls as indicated by both behavioural and ERPs measures. Although both M.X. and the controls showed the typical linear association between RTs and rotation angles, M.X. performed faster than the controls across rotation angles. In addition, the typical RRN modulation by rotation angle was found in the control but not in M.X., revealing that MX was not showing the correlate of MR proper on mirror letter trials. All these finding together suggest that M.X. could successfully complete the MR tasks without mentally rotating the mirror letters. This lack of evidence for MR processing in dealing with mirror images may be accounted by the decreased ability of M.X. to represent a vivid image in his mind's eyes. As VVIQ score was found highly correlated with the activation in early visual cortex in an fMRI study (Cui et al, 2007), M.X. who showed significantly lower VVIQ2 score as compared to his control participants may have a deficit in representing the image of mirror letters. Moreover, unlike the normal letters, it is difficult for one to read a letter

in its mirror version and to represent it in a language-like format. MR processing as a cognitive process happens sequentially after the generation of the stimulus representation (Heil, 2002; Stoffels, 1996) which is independent from the specific representation format, whether of depictive or language-like. Without the representation of mirror letters, the MR proper could not be carried out to complete the MR task.

This phenomenon of completing MR tasks in the absence of MR proper could be accounted by the different strategy adopted. Liesefeld and Zimmer (2013) provided behavioural and ERP evidence that spatial but not visual information is extracted from the visual stimuli to complete MR tasks. Therefore, it is possible that M.X. focused on the spatial feature extracted from the mirror letters (i.e. the arch in "P" or "R") and judge the parity based on its relative location (i.e. whether the arch is on the right or left side of the vertical line). An alternative account could refer to Cooper and Shepard's speculation on prepared response (1973) that M.X. prepared a 'mirror' response before the trial begins and made an execution once he found the abnormal of the visual stimuli (i.e. unable to read the mirror letters).

Notably, in the current experiment, M.X. showed the typical linear pattern of response times in both normal and mirror condition. This is different from the observation reported previously (Zeman et al., 2010) whereby M.X. was described as presenting with a non-linear pattern of response times with the increasing angles of rotation. This difference may be accounted for by the familiarity of the stimuli in the

current experiment. The canonical representation of over-learned characters, such as letters, can be retrieved from long-term memory, whereas extra cognitive resource may be required to encode and represent unfamiliar stimuli. M.X, could more likely show typical patterns, compared to controls, in processing the more complex MR tasks used in Zeman et al.'s study (2010) than the present experiment.

In sum, the current finding that M.X., the case of "blind imagination", could successfully complete the MR task with characters in the absence of depictive representation provides direct evidence for the debated issue regarding the format of representation and its role in MR tasks (e.g. Cooper & Shepard, 1973; Marmor & Zaback, 1976; Pearson & Kosslyn, 2015). M.X.'s differential performances in normal and mirror letters offers two possibilities for the issue how to complete MR tasks in the absence of depictive representation. In some cases, at least in processing familiar objects, like the normal letters which are highly accessible and encountered in everyday activities, MR processing could still be adopted but with a non-depictive mental representation (e.g., language-like). This finding provides supporting evidence for Pearson and Kosslyn's recent argument (2015) that multiple formats of representation could be generated for the same objects. For other cases, for example, in processing mirror letters in the current experiment, an alternative strategy might be adopted instead of MR processing to cope with MR tasks.

Chapter 3

Which properties of the Visual Stimuli predict Strategy in Mental Rotation?

3.1 Experiment 4 Introduction

The three experiments in Chapter 3 provided evidence for the argument that multiple formats of visual representations and strategies could be adopted in MR by exploring the differential performance across individuals with different levels of visual imagery vividness. This chapter aimed to provide more evidence for this argument from an alternative point of view by testing the hypothesis that different strategy selection could be adopted in different visual stimuli. Therefore, in Experiment 4, reported in the present chapter, we address this issue by assessing the research question which properties of the visual stimuli predict the strategy selection.

Polygons, instead of the character letters or Shepard and Metzler's cube stimuli (1971), were used as visual stimuli in the present experiment, as they were used in early work investigating this stimulus complexity hypothesis (e.g., Cooper, 1975).

Typically (Cooper, 1975; Cooper & Podgorny, 1976; Folk & Luce, 1987), the stimulus complexity was manipulated by changing the number of the vertices of the polygons (following Attneave & Arnoult, 1956). Therefore, we used polygons.

In this paradigm, participants were instructed to respond to rotated varies polygons and to discriminate whether they are identical or in mirrored version. The effect of complexity was found in some (Cooper, 1975; Cooper & Podgorny, 1976), which supported the view that holistic strategy was at play, but did not in some other studies (Bethell-Fox & Shepard, 1988; Yuille & Steiger, 1982), supporting the piecemeal transformation account.

This failure to find a complexity effect may have resulted from the fact that the required discrimination was always between a normal object and its mirrored image. That is to say, participants can do such discrimination based on a small set of information from the visual stimuli regardless of their complexity (Liesefeld & Zimmer, 2013). The possibility that the representation of visual stimuli could be simplified regardless of the complexity of the stimuli was supported by subsequent behavioural and ERP experiments (Yuille & Steiger, 1982; Liesefeld & Zimmer, 2013). Liesefeld and Zimmer (2013) assessed participants with simple, visually complex (with additional rotation-independent information) and complex stimuli (with additional rotation-dependent information) and found the visually complex objects could be rotated as efficiently as the simple ones and showed a much steeper slope than the complex stimuli.

To avoid the generation of this simplified representations, Cooper and Podgorny (1976) introduced an experimental manipulation whereby participants had to discriminate the canonical stimulus not only from its mirror version, but also from a set of distractors, which varied in their similarity with the target objects. It is assumed that in this situation participants have to encode all the information of the visual stimuli to successfully comply with the task. Whether the application of the distractors could successfully enforce participants to encode all the information in the visual stimuli is still unclear. Inconsistent results regarding this complexity effect were still reported in the experiments where participants have to discriminate not only between normal and mirror version, but also between normal and distractors (Cooper & Podgorny, 1976; Folk & Luce, 1987). Anderson (1978) suggested that even with distractors, when processing a complex object (i.e., polygons with twenty vertices) where too much information needs to be encoded, participants may fail to do so and instead generate a simplified representation of the stimuli. Folk and Luce (1987) manipulated the similarity of the distractors and found that the stimulus complexity effect was only reliable with highly similar distractors but not those with low similarity. These results provided a possible explanation for the inconsistent results.

However, it is worth noting that the stimulus similarity in Folk and Luce's experiment (1987) was based on the participants' subjective rating when they were asked to rate the similarity between the canonical and its distractors at upright position. Another group of participants' MR performances were analysed with these pre-defined

stimuli. The perceived similarity for the stimuli may vary from individual to individual and therefore may decrease the reliability of the pre-defined stimulus similarity. In addition, the stimulus complexity was only manipulated by changing the number of vertices (only 6- and 10-vertices polygons were used) of integrated polygons (see the following paragraph where the complexity could be manipulated by changing the number of perceptual distinct pieces). Whether and how the mismatch distractors work in MR with non-integrated stimuli is still to be determined.

Alternatively, the observed inconsistent results could be accounted for by the difference in how the stimulus complexity is manipulated. As described in the opening chapter and the introduction in Experiment 1, two variables are commonly adopted in the literature: 1) the number of components of an integrated object, such as the number of its vertices (e.g., polygons, Cooper & Podgorny, 1976 and Folk & Luce, 1987) and 2) the number of perceptually distinct pieces, such as the figure patterns in a matrix (Bethell-Fox & Shepard, 1988) or the number of segments in 3-D blocks (e.g., Yuille & Steiger, 1982). Bethell-Fox and Shepard (1988; see also Podgorny & Shepard, 1983) found that the number of distinct pieces correlated with RTs in MR. Accordingly, piecemeal transformation was suggested to be more likely to operate in multi-part objects (Yuille & Steiger, 1982; Shepard & Feng, 1972). However, to our knowledge, no study directly investigated the relationship between the properties of the stimuli and the strategy selection in MR tasks.

Therefore, the aim of the present experiment was to investigate which properties of visual stimuli predict the strategy selection in MR tasks. Firstly, which type of stimulus complexity manipulation is more likely to predict strategy selection, the vertices number or the number of segment? Secondly, the role of distractors in strategy selection in MR tasks. Polygons of increasing complexity were selected as the stimuli for this experiment, as they were used in Cooper's experiments (1976; Cooper & Podgorny, 1976) and in a series of ensuing studies investigating the complexity effect (e.g., Folk & Luce, 1987). A subset of six types of stimuli were selected with three different levels of vertices number (six, nine and twelve) and two levels of segment number (integrated vs. two-part; see top six rows in Figure 3-1). If a holistic strategy is used for integrated polygons as posited by Cooper (1975; and Cooper & Podgorny, 1976) whereas a piecemeal transformation is at play in the two-segment polygons, there would be a main effect of segments number and a steeper slope would show in the two-segment than the integrated polygons but with no main effect of vertices number. In addition, with-foil and without-foil conditions were introduced to test the role of distractors directly. If distractors have indeed the ability to enforce participants to encode all the information of the visual stimuli, there would be an effect of distractors. In addition, stimulus complexity effect would be found under with-foil condition but not the without-foil session.

3.2 Methods

3.2.1 Participants

Twenty-two participants (mean age = 21.5, range: 19 to 24 years old, ten women) were recruited for this experiment all of whom were students from University of Edinburgh who received study credits for their participation. All participants were right handed, with no history of neurological disorders and reported having normal or corrected-to-normal vision.

3.2.2 Stimuli

The stimuli were presented in white on a black background. They were 5.5 cm in height subtending 4.55° of visual angle. As shown in Figure 3-1, there were 12 experimental conditions in the current experiment with three variables being manipulated: 1) number of vertices; 2) number of segments and 3) with- or without-distractors. Two subsets of stimuli were selected separately to address the two set research questions.

To address the question about the role of distractors in MR performance, four types of polygons with twelve vertices were selected (see row 5 to 12 in Figure 3-1) in with- and without-foil conditions separately. The complexity of these twelve-vertices polygons were manipulated by changing the segment number (one, two, three and four). A self-written Matlab program was used to generate these stimuli by dividing the corresponding integrated object into two, three, or four segments while the vertices remained as in the prototype.

A set of distractors were generated (columns 4 to 7 in Figure 3-1), as in previous studies (Cooper, 1975; Cooper & Podgorny, 1976), for each canonical stimulus (the first column in Figure 3-1). A Matlab program was written to randomly perturb the coordinates of any point of the canonical stimuli with the amplitude ranged from 0.1 to 0.5. For each of the ten canonical polygon objects, 30 different perturbations were generated and four were selected for testing based on the following two criteria: 1) all segments/vertices in the stimuli were manipulated: a. in the integrated Six-vertices, Nine-vertices and Twelve-vertices polygons, four non-consecutive vertices were perturbed; b. in multi-part objects, at least one vertex was manipulated in each segment; 2) the similarity between the distractors and the canonical stimuli modulates the stimulus complexity effect (Folk & Luce, 1987); to avoid such effect, the similarity of the four selected distractors was counterbalanced by choosing two high- and two low-similarity perturbations. Their similarity was determined by the amplitude being perturbed and controlled for. The average perturbed amplitude is 0.27, and the similarity across the ten types of stimuli were roughly equal ($SE = .01$) (see Appendix B for details).

To investigate the question on which property of visual stimuli predicts strategy selection in MR tasks, another subset of stimuli was selected, which varies with vertices number (six, nine and twelve; six, nine and twelve[7]) and the segment

7 A selected range of vertices number were selected as compared to Cooper and Podgorny's experiment (1976) as partial image or small portion of information is suggested more likely

number (one or two). Therefore, six types of stimuli were designed as depicted on the top six rows in Figure 3-1 with their corresponding mirrored images and distractors.

For each stimulus type, a pair of objects was presented on the screen with three rotation angle (0°, 60° and 120°) either clockwise or counter clockwise (two orientations of rotation). In with-foil condition, as summarized in the first eight rows in Figure 3-1, three categories of paired stimuli were presented with a different orientation: 1) one object paired with an identical object; 2) one object with its mirrored object or 3) one object with one of its corresponding distractors. Identical pairs were presented on five instances whereas both the mirrored and four distractors were presented only once (see Figure 3-2). In without-foil condition as shown in the four bottom rows in Figure 3-1, two types of pairs were presented. In half of the trials one object was paired with an identical object in a different orientation, whereas in the other half its mirrored figure was presented still in a different orientation. Both identical and mirrored pairs were presented five times (see Figure 3-2). For each experimental condition as depicted in Figure 3-1, 60 trials were randomly presented in one block. All considered, 720 trials were included in this twelve-block experiment including eight blocks with distractors and the other four without distractors.

3.2.3 Procedure

to be used in processing the more complicated polygon with too many vertices (Anderson, 1978).

Participants were required to sit in front of a computer with the keyboard all masked except for two buttons marked “S” and “D”, indicating “same” and “different” respectively. For half of the participants, the “S” button was set on their right hand side and the “D” button on their left side. For the other half of the participants, the “S” button was set on their left side and the “D” on their right. During the whole procedure, the participants were asked to keep their hands on the keyboard.

Canonical	Vertices number	Segment number	Distractor condition	Distractor1	Distractor1	Distractor3	Distractor4	Mirror
	6	1	with					
	9	1	with					
	12	1	with					
	6	2	with					
	9	2	with					
	12	2	with					
	12	3	with					
	12	4	with					
	12	1	without					
	12	2	without					
	12	3	without					
	12	4	without					

Figure 3-1. Twelve types of stimuli used in the experiment. To the right of each canonical type are three measures of stimulus complexity (vertices number, segments number and distractor condition) and four types of distractors and mirrored image.

For each trial (see Figure 3-2), first a black screen was presented for 250ms, followed by a fixation cross lasting 200ms to 250ms then a pair of polygons were presented for 4,000ms or until participants responded. Participants were instructed to indicate whether these two objects were the same (identical though rotated) or different (mirrored or foil pairs in the with-foil condition or mirrored pairs in without-foil condition) by pressing the "S" or "D" button respectively.

The blocks were presented in random order for with- and without-foil sessions. The order of the two sessions were counterbalanced across participants. Before each session, a run-in of 15 trials served as a practice allowing participants to familiarize with the task. The polygon stimuli as well as the distractors were different from the ones used in the real experiment.

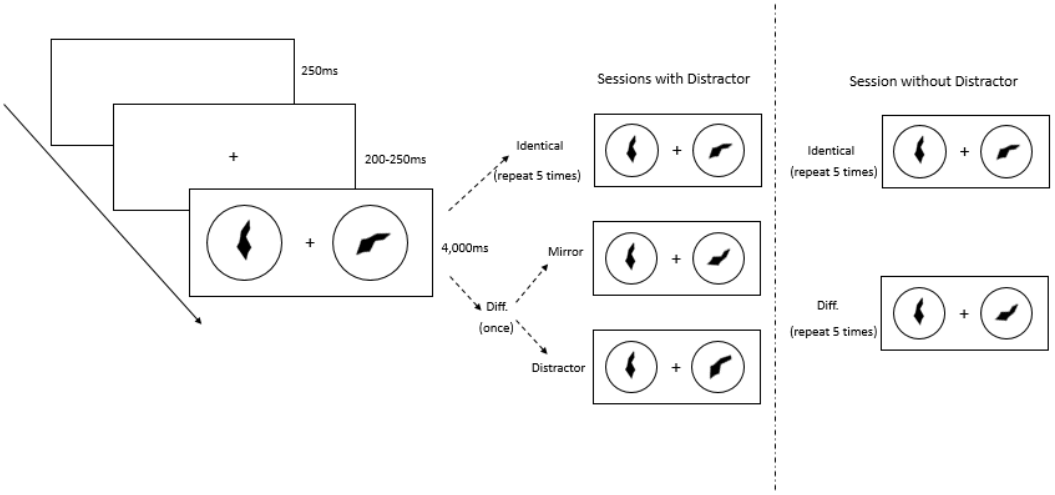

Figure 3-2. Experimental procedure. In the with-distractor session (middle panel), half of the trials were a pair of identical polygon stimuli with different rotation angles with five repetitions for each pair; in the other half trials, one canonical polygon stimuli was paired with its mirrored image or four types of corresponding distractors (presented once for each type). In the without-distractor session (right panel), half of the trials were a canonical stimuli paired with identical stimuli with different rotation angles, the other half were paired with its mirrored image. Both types were presented in five repetitions.

Participants were asked to fill in the VVIQ-2 (Marks, 1995) after the MR tasks[8].

3.2.4 Data analysis

Prior to the analysis, RTs data were trimmed for outliers. RTs that were more than two standard deviations above or below their mean value per condition and per participant were excluded (12.6% of the data on average). The results were analysed

[8] The VVIQ-2 scores were not factored in the data analyses for two reasons. First, in this sample, the scores were not normally distributed (Shapiro-Wilk test: $p = .02$). Moreover, the primary interest of this experiment was to explore whether/ how visual stimuli affect the strategy selection in MR tasks which is independent of VVI.

based on the identical trials only[9]. Gender was not included as a factor for data analysis[10]. Two subsets of stimuli were selected for data analysis to address the two questions set for the present study separately as summarized below.

To investigate the first question on which properties of the visual stimuli are more likely to predict the strategy selection in MR, two variables were firstly taken into account, namely vertices number and segment number. Six types of stimuli in the session with distractors (see top six rows in Figure 3-1) were considered[11]. A repeated-measures analysis of variance (ANOVA) was applied to the accuracy rate and the correct RTs with three within-subject factors: three levels of vertices number (six, nine and twelve), two levels of segment number (one and two) and three levels of rotation angle (0°, 60° and 120°). Trend analysis would be applied in each condition followed by Bonferroni corrected pairwise comparisons, once the main effect of rotation angle or vertices number was observed. We fitted a linear line to each participant's RTs in each experimental condition to calculate the slope and intercept of this line. A repeated-measures ANOVA was used to analyse the estimated slope and intercept

[9] It is typical to analyze the identical trials only (e.g. Metzler & Shepard, 1974) as differential neural mechanisms were suggested to underline identical and mismatched trials (Martinaud et al., 2016) and RTs for mismatched trials are harder to interpret because the rotation angle is not well defined.

[10] We ran the analysis of covariance (ANCOVA) with gender as a co-variate and found gender did not interact with all other factors, all *p*-values $\geq$ .045. Therefore, gender was excluded from the analyses reported in the present paper.

[11] It is impossible to involve three or four segments in the six- or nine-vertices polygons according to our design. Therefore, the stimuli with one or two segments were analysed for the first question.

measurements with vertices number and segment number as two within-subject factors. Whenever appropriate, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. Partial η^2-values for each significant main effects or interactions were reported as well as the corrected p-values.

To investigate the second question on whether and how distractors affect strategy selection in MR, an additional factor, distractors, was introduced in the analysis to directly compare the MR performance in with- and without-foil condition. The stimulus complexity was only manipulated by the number of segments. Therefore, the data of four types of twelve-vertices polygons with different segment number in with- and without-foil conditions (the bottom eight rows in Figure 3-1) were selected for analysis. A repeated-measures ANOVA was applied to accuracy and correct RTs with three within-subject factors: segment number (one, two, three and four), rotation angle (0°, 60° and 120°) and two levels of mismatched foil (with and without). Once the main effect of rotation angle was found, linear trend analysis would apply followed by Bonferroni corrected pairwise comparisons. We then fitted a linear line to each participant's RTs in each experimental condition to calculate the slope and intercept of this line. A repeated-measures ANOVA method was used to analysis the estimated slope and intercept measurements with two within-subject factors: segment number (one, two, three and four) and foil (with vs. without). Once segment number was found to affect either the slope or the intercept or to interact with the foil, linear trend analyses would apply in each experimental condition to test the effect of segment number.

3.3 Results for the first research question

Results are reported here below to address the first research question: which properties of the visual stimuli are more likely to predict the strategy selection in MR, vertices number or segment number?

3.3.1 Accuracy

A main effect of segment number was observed in the accuracy rates, F (1, 21) $= 8.35$, $p = .009$, $\eta^2 = .28$. The accuracy rate in processing the two-segment objects (mean $= 81.3\%$, SE $= 2.4$) was significantly poorer than that in processing the integrated objects (mean $= 86.9\%$, SE $= 2.1$). A main effect of vertices number was also found, F (2, 42) $= 9.43$, $p < .001$, $\eta^2 = .31$. Trend analysis confirmed that the accuracy rate linearly increased with the increasing vertices number, F (1, 21) $= 21.87$, $p < .001$, $\eta^2 = .51$. Post-hoc analysis with Bonferroni correction revealed that the accuracy rate in processing six-point polygons (mean $= 78.7\%$, SE $= 2.1$) was significantly poorer than that in processing both nine-point (mean $=86.7\%$, SE $= 2.8$), $p = .008$, and twelve-point polygons (mean $= 87.0\%$, SE $= 1.8$), $p < .001$.

Consistent with previous literature, a main effect of rotation angle was observed, F (2, 42) $= 42.41$, $p < .001$, $\eta^2 = .67$. Confirmed by linear trend, the linearly decrement was observed in accuracy rates with the increasing rotation angle, F (1, 21) $= 13.94$, $p = .001$, $\eta^2 = .40$. The Bonferroni-corrected planned comparison showed that accuracy rate in processing the polygons in the up-right position (0°; mean

$= 95.6\%$, SE $= 1.8$) was significantly greater than that in processing the 60° rotated stimuli (mean $= 80.0\%$, SE $= 2.5$), $p < .001$, as well as the 120° rotated ones (mean $= 76.7\%$, SE $= 2.8$), $p < .001$. No interaction was observed in the accuracy rate (segment number × rotation angle: F (2, 42) $= 1.52$, $p = .231$; vertices number × rotation angle: F (4, 84) $= 2.07$, $p = .093$; segment number × vertices number × rotation angle: F (4, 84) $= 2.29$, $p = .066$).

3.3.2 Response times

RTs data are summarized in the left panel of Figure 3-3. As expected, significant longer RTs were observed in processing two-segment polygons (mean $=$ 1938.9ms, SE $= 79.3$) compared to the integrated ones (mean $= 1609.6$ms, SE $=$ 87.4; see Figure 3-3), F (1, 20) $= 57.07$, $p < .001$, $\eta^2 = .74$. However, no main effect of vertices number was found, F (2, 40) $= .80$, $p = .073$.

A main effect of rotation angle was found in RTs, F (1.5, 30.7) $= 154.51$, $p < .001$, $\eta^2 = .89$. As reported in the previous literature, the RTs increased with the increasing rotation angle in a linear trend, F (1, 20) $= 219.21$, $p < .001$, $\eta^2 = .92$. Revealed by post-hoc analyses with Bonferroni correction, significantly longer RTs were observed in processing the stimuli at 120° (mean $= 2088.5$ms, SE $= 90.6$) compared to those in smaller rotation angle (0°, $p < .001$; 60°, $p < .001$); RTs in processing the stimuli at 60° (mean $= 1948.2$ms, SE $= 95.2$) was observed significantly longer than that in the upright position (0°; mean $= 1286.0$ms, SE $=$ 67.6), $p < .001$.

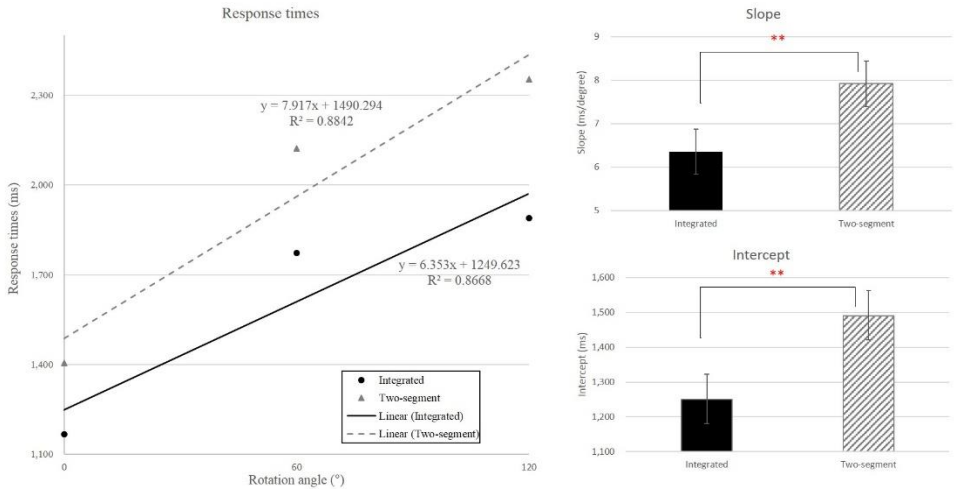

Figure 3-3. Performance in six types of polygon stimuli with two-level segments number and three-level vertices number. Left panel depicts the response times across all rotation angles; top right panel presents the estimated slope whereas bottom right panel shows the intercepts.

3.3.3 Slopes

A main effect of segment number was observed in the estimated slope measure, F (1, 21) = 7.01, p = .015, η^2 = .25. As shown in Figure 3-3, the top right panel, a steeper slope was observed in RTs when processing the two-segment polygons (mean = 6.4ms/degree, SE = 0.5) compared to that in processing the integrated ones (mean = 7.9ms/degree, SE = 0.6).

However, no main effect of vertices number was found in this estimated slope measure, F (2, 42) = .44, p = .650. Furthermore, there was no vertices number × segment number interaction, F (2, 42) = .76, p = .476.

3.3.4 Intercepts

Intercepts are depicted in the bottom right of Figure 3-3. A main effect of segment number was found in the estimated intercept, F (1, 21) = 34.14, $p < .011$, $\eta^2 = .62$. Longer times were needed in encoding the stimuli or in giving response in two-segment polygons (mean = 1490.3ms, SE = 69.6) than those in integrated ones (mean = 1249.6ms, SE = 72.8). No main effect of vertices number was observed in the slope measure, F (2, 42) = 2.23, $p = .120$.

However, vertices number was found to interact with segment number in the intercept measure, F (2, 42) = 13.58, $p < .001$, $\eta^2 = .39$. A repeated-measures ANOVA method was applied to the integrated polygons (segment number = 1) and two-segment polygons (segment number = 2) separately. In processing the integrated polygon stimuli, there was a main effect of vertices number in the intercept, F (2, 42) = 11.90, $p < .001$, $\eta^2 = .36$. Confirmed by the trend analysis that the intercept linearly increases with the vertices number in the polygon stimuli, F (1, 21) = 18.61, $p < .001$, $\eta^2 = .47$. Post-hoc analyses with Bonferroni correction revealed that significantly longer time was spent in either stimuli encoding or giving responses with the polygons with twelve vertices (row five in Figure 3-1; mean = 1443.2ms, SE = 110.5) than in the polygons with nine vertices (row three in Figure 3-1; mean = 1224.1ms, SE = 69.8), $p = .015$, or with six vertices (row one in Figure 3-1; mean = 1081.6ms, SE = 66.3), $p < .001$. On the other hand, in processing the two-segment polygons, no vertices number effect found, F (2, 42) = 1.64, $p = .206$, $\eta^2 = .07$, suggesting that the vertices number did not affect the sub-phase in either stimuli

encoding or giving responses in two-segment polygon stimuli, in which piecemeal transformation was likely at play.

3.4 Results for the second research question

The results reported below were addressed the second research question raised in the present experiment to explore the role of distractors in strategy selection in MR tasks.

3.4.1 Accuracy

A main effect of segment number was observed on the accuracy r ates, F (2.4, 49.6) $=$ 13.83, $p < .001$, $\eta_p^2 = .40$. This was confirmed by trend analysis showing that the accuracy rates linearly decreased with the increasing segment number, F (1, 21) $=$ 29.41, $p < .001$, $\eta_p^2 = .58$. Post-hoc analysis with Bonferroni correction further revealed that the accuracy rate in processing the two-segment polygon (mean $=$ 87.5%, SE $=$ 2.0) remains similar to that in the integrated polygon (mean $=$ 87.7% , SE $=$ 2.2). However, the accuracy dropped dramatically, from the average accuracy at 87.7% $\pm$ 2.2 in two-segment polygons to that at 82.7% $\pm$ 2.8 in three-segment polygons, $p = .003$, and at 77.8% $\pm$ 2.9 in four-segment polygons, $p < .001$. However, no main effect of foil was found, F (1, 21) $=$ 2.41, $p =$ .135.

Consistent with previous literature, a main effect of rotation angle was found in the accuracy, F (2, 42) $=$ 49.07, $p < .001$, $\eta_p^2 = .70$. As indicated by trend analysis, the accuracy decreased linearly with the increasing segment number, F (1,

21) = 64.67, $p < .001$, $\eta_p^2 = .76$. Post-hoc analysis with Bonferroni correction revealed that the accuracy dropped from 95.1% ± 1.8 at up-right position (0°) to 81.7% ± 2.7 at 60°, $p < .001$, and continued drop till 75.0% ± 3.0 at 120°, $p = .006$.

While no other interaction found in the accuracy rate (foil × segment number: F (2.192, 46.039) = .232, $p = .813$, $\eta_p^2 = .011$; foil × rotation angle: F (2, 42) = 0.92, $p = .407$, $\eta_p^2 = .04$; foil × segment number × rotation angle: F (6, 126) = 1.29, $p = .268$, $\eta_p^2 = .06$), the interaction of segment number and rotation angle was detected, F (6, 126) = 2.06, $p = .021$, $\eta_p^2 = .11$. By analysing the estimated slopes and intercepts in the accuracy rate, we found the following results with regard to the segment number × rotation angle interaction: there was no effect of segment number found on the intercept in the accuracy rates, F (2.0, 43.9) = 1.94, p = .132, $\eta_p^2 = .08$; however, such segment number effect was found in the slope measure, F (2.0, 43.2) = 4.96, $p = .012$, $\eta_p^2 = .18$, which fitted with a linear trend, F (1, 22) = 7.45, $p = .012$, $\eta_p^2 = .25$.

3.4.2 Response times

The RTs under different stimuli types are reported in the left panel in Figure 3-4. Segment number of the stimuli affected the RTs in MR tasks, F (3, 63) = 21.27, $p < .001$, $\eta_p^2 = .50$. Trend analysis further indicated that the RTs were linearly increased with the increasing segment number, F (1, 21) = 37.84, $p < .001$, η_p^2

= .64. Significant longer RTs were observed in processing the stimuli with three segments (mean = 1995.2ms, SE = 75.1) comparing to the integrated ones (mean = 1749.4ms, SE = 74.8), $p = .009$, as well as those consisted of two segments (mean = 1670.3ms, SE = 69.9), both ps $\leq .001$. In addition, longer RTs were observed in processing the four-segment polygons (mean = 2182.8ms, SE = 89.2) than in the ones with three segments, $p = .043$. A main effect of foil was also found in the RTs, F (1, 21) = 16.63, $p = .001$, $\eta_p^2 = .44$. As expected, significant longer RTs were required in with-foil condition (mean = 2075.6ms, SE = 92.3) than in the without-foil one (mean = 1723.3ms, SE = 58.2).

As reported in previous literature, there was a main effect of rotation angle in the RTs, F (2, 42) = 336.26, $p < .001$, $\eta_p^2 = .94$. As verified by trend analysis, RTs were linearly increased with the increasing rotation angle, F (1, 21) = 624.24, $p < .001$, $\eta_p^2 = .97$. RTs in processing the stimuli at 60° (mean = 2034.2ms, SE = 75.4) were significantly longer than in processing those in the upright position (at 0°; mean = 1358.6ms, SE = 66.5), $p < .001$. Significantly longer RTs were observed in processing the stimuli at 120° position (mean = 2305.6ms, SE = 59.7) than those rotated at 60°, $p < .001$.

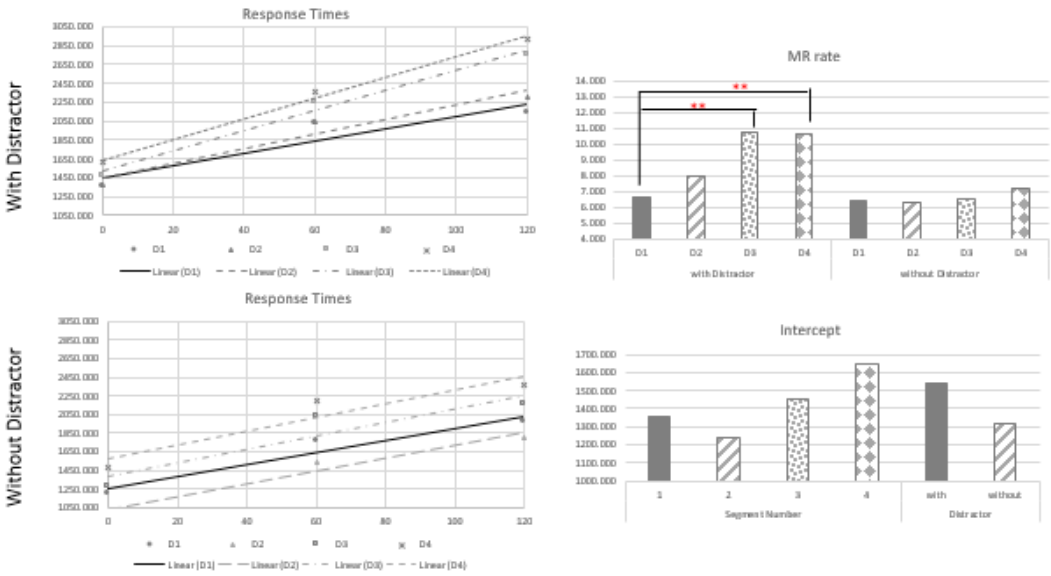

Figure 3-4. Performance in eight types of polygon stimuli in with- and without-distractor conditions. Left panel depicts the response times across all rotation angles; top right panel presents the estimated slope whereas bottom right panel shows the intercepts.

3.4.3 Slopes

A main effect of segment number was observed in the slope measure, F (3, 63) = 5.34, p = .002, η_p^2 = .20. Slower MR rate was observed in processing the stimuli with more segments. Trend analysis further indicated that the MR rate became linearly slower with the increasing number of segments, F (1, 21) = 162.17, p = .001, η_p^2 = .43. The MR rate in processing the four-segment polygons (mean = 8.9ms/degree, SE = 0.6) was significantly slower than that in processing the integrated ones (mean = 6.5ms/degree, SE = 0.4), p = .012.

In addition, there was a main effect of foil on the slope measure in the RTs function of rotation angle, F (1, 21) = 34.10, p < .001, η_p^2 = .62. In the without-foil

condition (mean = 6.6ms/degree, SE = 0.3), participants performed much faster as compared to their performance in the with-foil condition (mean = 9.0ms/degree, SE = 0.4).

The interaction of foil and segment number was also found in this estimated slope measure, F (3, 63) = 3.31, p = .026, η_p^2 = .14. Repeated-measures ANOVA method was applied on the slope measure in with- and without- foil condition separately. As depicted in the top right panel in Figure 3-4, the effect of segment number was evident on the slope measure in with-foil condition, F (3, 63) = 5.91, p = .001, η_p^2 = .22. Trend analysis further indicated that the MR rate linearly decreased with the segment number, F (1, 21) = 19.25, p < .001, η_p^2 = .48. The MR rate in processing either the three-segment (mean = 10.7ms/degree, SE = 0.9) or four-segment polygons (mean = 10.6ms/degree, SE = 1.0) was significantly slower than that in processing the integrated ones (mean = 6.7ms/degree, SE = 0.6), both $p \leq$ .008. On the other hand, in the without-foil condition (see the bottom panel in Figure 3-4), no effect of segment number was observed, F (3, 63) = .58, p = .634, η_p^2 = .03, suggesting that holistic strategy was applied in this condition.

3.4.4 Intercepts

A main effect of segment number was found in the estimated intercept measure in the RTs function of rotation angle, F (3, 63) = 14.69, p < .001, η_p^2 = .41. The time spent in either stimuli encoding or giving responses proved to increase linearly with the segment number, F (1, 21) = 19.62, p < .001, η_p^2 = .48. The time to process

the four-segment stimuli (mean = 1646.2ms, SE = 101.2), either at encoding or in giving response, was significantly longer than the time spent in processing the two-segment stimuli (mean = 1242.0ms, SE = 63.9), $p < .001$, or the integrated polygons (mean = 1359.2ms, SE = 73.5), $p = .007$. In addition, the mismatched foil was observed to affect the intercept, F (1, 21) = 6.03, $p = .023$, $\eta_p^2 = .22$. As expected, less time was required in either stimuli encoding or giving responses in the without-foil condition (mean = 1314.5ms, SE = 59.0) than in the with-foil condition (mean = 1537.3ms, SE = 100.3).

3.5 Discussion

In the present study, two questions were raised: 1) which properties of the objects are more likely to influence the strategy selection in MR tasks; and 2) would distractors play any role in strategy selection in MR tasks. By manipulating the complexity level of the polygon stimuli, the slopes in RTs function of rotation angle were tested directly to indicate the strategy applied in MR tasks as Cooper suggested (1995; see also Cooper & Podgorny, 1976).

To address the first question, the effect of vertices number as well as the effect of their segment number in polygon stimuli were tested. The current finding that the segment number rather than vertices number has the main effect on the slope measure, which suggests that the manipulation of segment number in an object rather than the number of its vertices is more likely to influence the strategy selection in MR (Cooper,

1975; Cooper & Podgorny, 1976). This finding resonates with the outcome of the first experiment reported by Bethell-Fox and Shepard (1987; see also Podgorny & Shepard, 1983). In their study, the number of shaded squares and the non-adjacent pieces was manipulated within a 9×9 matrix. The number of non-adjacent pieces rather than the number of shaded squares correlated with RTs. One possible explanation suggested for such correlation is that longer RTs were required to transform each of the multi-part stimuli than to transform the integrated piece. The present study provided direct evidence for this hypothesis.

In addition, in previous studies (Bethell-Fox & Shepard, 1987; Podgorny & Shepard, 1983), stimuli were restricted to rotate 90 or 180 degrees. One may argue that these two specific angles could be solved by alternative cognitive processes (at least by some participants; Cooper & Shepard, 1973; Liesefeld & Zimmer, 2011). For example, "flip over" strategy is suggested in processing stimuli in 180 degree instead of MR (Murray, 1997; Just & Carpenter, 1985). Liesefeld and Zimmer (2011) raised another possibility that the representation is first flipped along the horizontal and then along the vertical axis to comply with the 180°-rotated images. To explore the effect of stimulus complexity on a more general strategy selection in MR tasks, these two specific angles were avoided in the present study and stimuli were rotated either at either 60 or 120 degree instead.

In MR with integrated objects, no effect of vertices number was found on the estimated slope measure. According to Cooper's hypothesis (1975), this finding

suggests the holistic strategy was at play in integrated objects. This is consistent with Cooper and Podgorny's (1976) study in which pure rotation times were analysed and found to be independent of the stimulus complexity. Folk and Luce (1987), however, combined the RTs with identical trials as well as those accompanied with a foil and found an interaction between stimuli similarity and complexity. The complexity effect was only observed when the distractors were similar to the canonical ones. It is possible that different cognitive processes are called upon to process trials with an identical object and those with a foil. Additional time and resources may be needed for discriminating the difference between canonical stimuli and their distractors. In this context, the interaction of stimulus complexity and similarity on RTs found in Folk and Luce (1987) may not reflect the pure mental rotation process but is probably caused by the different RTs in discriminating canonical stimuli and their highly similar distractors. Detailed and specific differences would need to be detected and more time would be required for more complex objects. On the contrary, it would be easier to detect the difference between canonical stimuli and their less similar distractors; consequently, RTs would be independent of the stimulus complexity.

In addition, a steeper slope was found in processing the multi-part objects compared to that observed in processing the integrated ones. This result reveals that to process multi-part objects will slow the rotation rate. It is possible that participants mentally operate on stimuli consisting of perceptually distinct parts by considering one part at a time (Yuille & Steiger, 1982; Shepard & Feng, 1972). The specific format of

such representation in this piecemeal transformation is still unclear (Pearson & Kosslyn, 2015). For example, in the two-segment polygons participants could maintain the vertices and their relative locations and then transform the image vertex-by-vertex, or they could maintain each segment as an independent representation and transformed the stimulus segment-by-segment. No effect of vertices number was found in two-segment polygons, providing evidence that participants did not transform the individual vertices in their minds' eyes to comply with the tasks at least for these stimuli.

An alternative explanation for these findings refers to Liesefeld and Zimmer's account (2013) suggesting that independently of the stimulus complexity, only one piece per stimulus is rotated in MR tasks with integrated objects. Additional rotation-irrelative information might be encoded in multi-part stimuli and therefore slow down the rotation rate. However, it is notable that participants in the present study not only needed to discriminate the normal letters from their mirror images, but also from the distractors. As shown in Figure 3-1, these distractors were designed by randomly changing the relative location of the vertices. Hence, several spatial features have changed, especially for those stimuli with fewer vertices. Therefore, in the current MR experiment it would be difficult for the participants to extract the rotation-related information from the visual stimuli in a limited time to use them for MR processing.

As to the second research question about the role of distractors in strategy selection in MR, distractors in the present study affected the processing time as found

in Folk and Luce's (1987). Longer RTs were observed in processing the stimuli with distractors than those without. The analysis on the estimated slope indicated a faster MR rate in without-foil condition compared to that in the with-foil condition. In addition, distractors interacted with segment number on the estimated slope measure. Complexity effect emerged in the with-foil condition but not in the without-foil condition. This finding was consistent with the observations in the literature (Bethell-Fox & Shepard, 1988; Cooper & Podgorny, 1976; Yuille & Steiger, 1982) and provided a possible explanation for the inconsistent results.

In processing the stimuli without distractors, no effect of vertices number occurred. This suggested that in the without-foil condition, participants may ignore the stimulus complexity and automatically simplify the task by encoding partial image (Yuille & Steiger, 1982) or rotation-related information (Liesefeld & Zimmer, 2013) and maintain this simplified internal representation for further mental manipulation. By contrast, in the with-foil condition, the stimulus complexity effect was observed. Steeper slopes were observed in processing the three- and four-segment objects than that in integrated ones. These results, based on Cooper's complexity effect hypothesis (1975), suggested that piecemeal transformation was at play in processing these multi-part stimuli in MR tasks whereas holistic strategy was by default applied in processing integrated object. The format of these partially transformed representations is unclear. It is possible that the image of the segment polygons was stored and transformed. Alternatively, the spatial rotation-related information could also be represented and

transformed (Liesefeld & Zimmer, 2013). No matter with which format of representation, the functional role of the distractors was confirmed to increase the probability that participants encode more, or even all, the information of the visual stimuli. This is in accordance with Liesefeld and Zimmer's suggestion (2013) that the amount of information is not only based on the complexity of the rotated stimuli, but also on the type of comparison required. Therefore, more information has to be encoded to comply with the task, not only to discriminate between normal letters from mirror images, but also from the distractors. In addition, to cope with the more complex task with distractors, participants might be more careful to avoid errors; encoding more information of the visual stimuli would then result in slower MR rates. The MR rates, however, in rotating an integrated object and that in two-segment ones were comparable. These results provide evidence supporting the argument that participants could maximally bind two segments of the stimuli in their mind's eyes for transformation in MR tasks (Xu & Franconeri, 2015).

Combined with our previous findings where the cube numbers in Shepard and Metzler's typical arm-like objects did not affect the strategy selection (Zhao & Della Sala, 2018), we could postulate that the manipulation of complexity level of integrated objects does not change the strategy selection in an MR task. In addition, the introduction of distractors indeed plays a role in MR tasks. In the with-foil condition, participants processed the stimuli slower than in the without-foil condition and showed a significant stimulus complexity effect on the estimated slope. In this context, the

distractors indeed enforced participants to encode all the information in their mind's eyes (see Cooper & Podgorny, 1976). However, no stimulus complexity effect was found, which suggests that participants have the ability to simplify their mental representations of the visual stimuli automatically for the further mental transformation.

All considered, the current finding provides a good reason for future MR studies to manipulate the stimulus complexity by changing the segment number rather than the vertices number involved if polygons were selected as stimuli. Moreover, adding distractors might avoid participants encoding partial or selected information for MR processing. Although the significance levels are reliable, the relatively small sample size is another possible limitation of the current study. Future studies could also be carried out based on the current findings to explore other potential factors (i.e., gender or spatial ability) that might affect the default strategy used in MR tasks.

Chapter 4

Ageing effect on Mental Rotation

In the light of the idea that the strategy selection in MR tasks may vary with individuals, as we explored by the three empirical experiments presented in Chapter 3, we were interested to explore whether this difference in strategy selection could account for the well-studied ageing effect in MR. Therefore, this chapter focuses on exploring the ageing effect on MR tasks. Slowing performance was largely documented in MR with old adults in the literature (Band & Kok, 2000; Cerella, Poon & Fozard, 1981; Jacewicz & Hartely, 1987; Thomas, 2016). This age-associated slowing has been addressed from two aspects: (1) the slowing MR rate with age indicated by the steeper slope; and (2) the slowing with age in non-rotation process (es) indicated by the larger intercept. In experiment 5 and experiment 6, the MR rate is analysed in younger and older adults to test our hypothesis that this age-related slowing could be accounted by the different strategy selection. On the other hand, the larger intercept observed in the older in behavioural experiment represent the speed of

responses in the absence of MR, encompassing two distinct cognitive processes, the early phase of stimuli encoding/ identification and the late phase of partial judgement and responses execution. Thus, the aim of experiment 7 was to further explore whether the initial phase of MR will slow with age by analysing time course of younger and older adults in a letter rotation task.

4.1 Experiment 5

4.1.1 Introduction and brief recap

As discussed in the opening chapter (see section 2.4.2 for detail), the typical linear increment of RTs with rotation angle was consistently observed in the older as in younger adults. Moreover, an age-associated slowing was observed in the MR rate especially in processing unfamiliar objects as indicated by the steeper slope observed in the older than that in young adults (Gaylord & Marsh, 1975; Hertzog & Rypma, 1991; Puglisi & Morrell, 1986).

Although this systemic slowing of MR rate with age may be explained by the general decreased cognitive ability in older adults or their decreased memory ability, the present experiment set up is to address another possibility: can differences in rotation strategies explain the age differences observed in MR rates? Few studies to date have explicitly manipulated the effect of stimulus complexity with the aim of investigating the rotation strategies employed by younger and older individuals. Dror, Schmitz-Williams and Smith (2005) assessed the performance of younger and older

participants in a MR experiment with two-dimensional (2D) drawings of familiar objects (e.g., a helicopter or a house) with different levels of complexity. Stimulus complexity was quantified by calculating the compactness of the drawing (see e.g., Podgorny & Shepard, 1983). Simpler stimuli had a higher compactness value while more complex stimuli had a lower compactness value. Younger participants used a holistic strategy in processing simple objects but swapped to a piecemeal transformation in processing complex ones, showing a steeper slope. On the contrary, older participants processed both simple and complex objects in a similar manner. The authors interpreted this lack of complexity effect in older participants as evidence that they maintained a holistic strategy while processing both simple and complex objects, because this strategy poses less demands on cognitive resources, including their ability to memorize and mentally manipulate the objects.

While this study provides initial evidence for systematic differences in strategy selection between younger and older individuals, it is worth noting that holistic processing is more likely to be adopted when the stimuli are familiar or over-learned (Bethell-Fox & Roger, 1988). It remains to be established whether analogous strategy differences would be observed with unfamiliar objects. The present study investigated for the first time whether age-related slowing in MR rates could be accounted for in terms of the difference in strategies that younger and older people may use to solve MR tasks with unfamiliar objects with different levels of complexity.

In the present study, participants were asked to rotate unfamiliar objects. Stimulus complexity was manipulated by increasing the number of segments that constituted them (integrated vs. multi-part objects). We predicted that younger participants would be flexible in manipulating their visual representations for complex stimuli and more efficient in rotating those by showing a shallower slope in their RTs as compared to simple stimuli where holistic strategy would apply in line with existing evidence (Yuille & Steiger, 1982). On the other hand, if older participants select the same strategy to rotate both simple and complex objects as previously observed for familiar stimuli (Dror et al., 2005), no stimulus complexity effect would be observed in the present study during the mental rotation of unfamiliar objects. However, processing unfamiliar objects poses additional cognitive demands as compared to familiar ones because participants cannot rely on the objects' stored visual representations. Thus, older participants might have selective difficulties in representing the whole image of complex unfamiliar objects and might adopt different strategies to rotate simple and complex unfamiliar objects.

4.1.2 Method

4.1.2.1 Participants

Twenty-four younger and twenty-four older participants were recruited for this experiment. One younger and three older participants were excluded due to their overall low accuracy ($< 50\%$). Younger participants were all students recruited from

the University of Edinburgh and all older participants were educated at university level and volunteered to participate. All participants were right-handed, with no history of neurological disorders. They all had normal or corrected-to-normal vision by self-report.

Both younger and older participants were given the VVIQ2 (Marks, 1999; see Appendix A for detail). The VVIQ-2 scores were numerically slightly higher in older (range: 78-159; mean = 143.24; SD = 20.9) than those of younger adults (range: 81-158; mean = 131.13; SD = 20.7); however, this difference fell short of significance, t (42) = -1.93, p = .06. In addition, the VVIQ-2 scores were normally distributed in younger (Shapiro-Wilk test: p = .138) but not in older adults (Shapiro-Wilk test: p < .001). Therefore, we did not consider this factor in the data analyses.

4.1.2.2 Stimuli

Two types of stimuli (Standard and non-Standard) with different complexity levels were used in the present experiment. Both Standard and non-Standard stimuli consisted of ten cubes. The Standard stimuli (top row in Figure 4-1) were the typical three-dimensional (3D) cube objects often used in MR experiments (Shepard & Metzler, 1971). The design of the non-Standard stimuli, was different from that used in Experiment 1 (see Figure 1-1c and Figure 1-1d). In Experiment 1, the non-Standard objects were designed by withdrawing two cubes from the Standard stimulus, so that a similar configuration characterized both standard and non-standard stimuli. However,

participants might have mentally filled the missing cube spontaneously on non-Standard trials. In this case stimuli could be considered as volumetric primitives. Therefore, we used a different stimuli design to prevent this possibility.

As depicted on the bottom row of Figure 4-1, the non-Standard stimuli used in this experiment were devised by decomposing the arms of the Standard stimuli and moving them away from the main body part. Compared to Standard stimuli, the less compact non-Standard stimuli are assumed to be harder to rotate holistically (Podgorny & Shepard, 1983).

On each trial a pair of objects was presented with different rotation angle ranging between 0° and 160° with 40° increments (rotation angle: 0°, 40°, 80°, 120°, 160°). Stimuli could be rotated along two axes, picture plane or in depth. On half of the trials, the two objects were identical whereas on the remaining half one object was paired with its mirror image (version: normal or mirror). In each block, there were 20 types of trials (5 rotation angle $\times$ 2 stimulus version $\times$ 2 rotated axis) each repeated 10 times. Two blocks of 200 randomly presented trials were presented separately for Standard and non-Standard stimuli. The sequence of these two blocks was counterbalanced across participants in each ageing group.

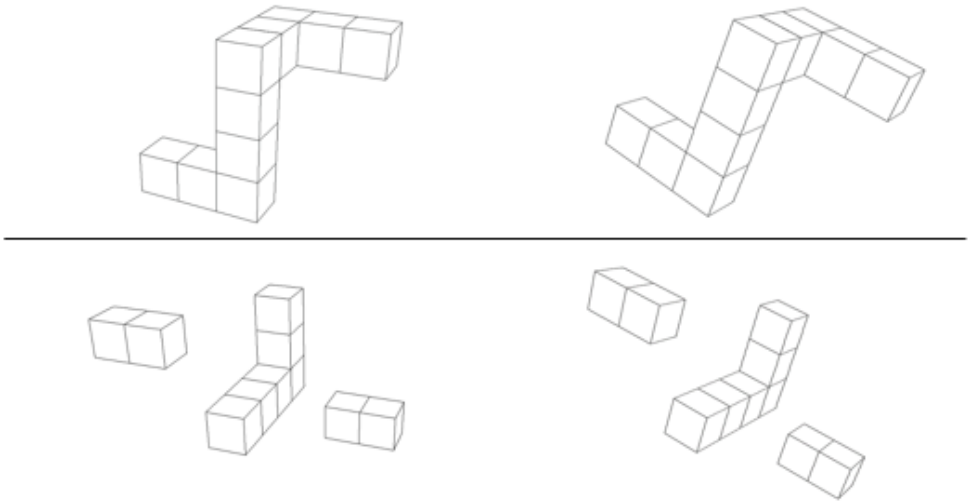

Figure 4-1. Two types of stimuli used in Experiment 4. Top row depicts an example of Standard stimuli; bottom row depicts the non-Standard stimuli used in Experiment 4 which were designed by decomposing the arms in the Standard stimuli and moved them away from the main part.

4.1.2.3 Procedure

Participants sat in front of a computer with their index fingers positioned on the keys “F” and “J” of a standard qwerty keyboard (used to respond to the stimuli). All keys were masked except for the two task relevant keys which were marked by the letters “S” and “D”, indicating “same” and “different” respectively. For half of the participants, the “S” button was set on their right-hand side and the “D” button on their left side. For the other half of the participants, the “S” button was set on their left side and the “D” on their right. The stimuli were presented in white on a black background with 5.5 cm in height subtending 4.55° of visual angle.

Each trial started with a blank white screen for 250ms, followed by a fixation cross (black on white background, 1.0 cm × 1.0 cm presented for a random interval ranging between 200-250ms. After the offset of the fixation cross, a pair of stimuli were presented on a white screen until the participant responded and maximally for 8,000ms. After 1,500ms the next trial began. Participants had to indicate whether the two objects were the same (normal though rotated) or mirror images, by pressing one of the two response keys. During the entire procedure, the participants were asked to keep their hands on the keyboard. Each block was followed by a debriefing session, in which participants orally reported on the strategy they used in the previous block.

A run-in of 16 trials served as practice allowing participants to familiarize with the task before each block. Instead of the ten-cube stimuli used in the experiment proper (see Figure 4-1), eight-cube Standard and non-Standard objects were used in these run-in trials to avoid the practice effect.

4.1.2.4 Data Analysis

As is typical in studies of MR, statistical analyses were carried out on normal trials only for assessing strategy selection in the younger as well as the older. Prior to the analysis, trials with reaction times exceeding two standard deviations above or below the mean per condition and per participant were excluded (2.3% of the data, on average). Mixed ANOVAs were carried out on both the mean RTs of correct responses and the average accuracy rates with rotation angle (0°, 40°, 80°, 120°, 160°) and stimulus complexity (Standard and non-Standard) as within-subject factors and age

(younger or older) as a between-subject factor. Trend analyses were considered when a main effect of rotation angle was observed and Bonferroni-corrected post-hoc analyses were performed to analyse the difference between two consecutive rotation angles. Whenever appropriate degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

As the aim of the present experiment was to investigate how ageing affects the strategy selection in unfamiliar object MR, a linear line was inserted into individual participants' mean RTs in each experimental condition to calculate the estimated slope and intercept. Mixed ANOVAs were applied to these two measurements with age (younger vs. older) as a between-subject factor and stimulus complexity (Standard vs. non-Standard) as a within-subject factor. When age was found to interact with stimulus complexity, independent t-tests were first applied to each experimental condition to explore the ageing effect in each condition. To further characterize the strategies applied in different conditions by different age group, the effect of stimulus complexity was further tested with paired t-tests in each age group. Bonferroni corrections were applied to control for the familywise error rates for multiple comparisons (McDonald, 2007).

4.1.3 Results

4.1.3.1 Accuracy

A main effect of rotation angle was found in the accuracy rates, F (2.4, 101.5) $=$ 40.14, $p < .001$, $\eta^2 = .49$. The accuracy rate linearly decreased with the rotation angle, F (1, 42) $=$ 77.25, $p < .001$, $\eta^2 = .65$. Furthermore, a main effect of stimulus complexity was found, F (1, 42) $=$ 7.46, p = .009, $\eta^2 = .15$. Performance was more accurate on trials with Standard (M $=$ 77.3%, SE $=$ 2.2) than non-Standard stimuli (M $=$ 70.6%, SE $=$ 1.8). In addition, younger participants' performance was more accurate (M = 81.5%, SE = 2.2) than older participants' one (M $=$ 66.5%, SE $=$ 2.3) as revealed by a main effect of age group, F (1, 42) $=$ 22.47, $p < .001$, $\eta^2 = .35$. However, no differential performance across the age groups was observed when processing the Standard and non-Standard objects, F (1, 36) $=$ 1.87, $p = .18$, through all the rotation angles in each condition neither, F (3.2, 113.4) $=$ 2.08, $p = .10$.

4.1.3.2 Response Times

The performance across younger and older participants is depicted in Figure 4-2. Consistent with the literature (Shepard & Metzler, 1971), a main effect of rotation angle was observed in the RTs, F (2.6, 110.5) $=$ 46.36, $p < .001$, $\eta^2 = .53$, which fitted a linear trend, F (1, 42) $=$ 14.20, $p = .001$, $\eta^2 = .25$. A main effect of stimulus complexity was also found in the RTs, F (1, 42) $=$ 14.20, $p = .001$, $\eta^2 = .25$. Slower RTs were observed in the processing of the non-Standard objects (M = 4975.26ms, SE $=$ 274.7) than in the Standard ones (M $=$ 4203.31ms, SE $=$ 240.1).

As shown in the left panel of Figure 4-2, a main effect of age was found in the RTs, F (1, 42) = 51.91, $p < .001$, $\eta^2 = .55$. Younger participants were faster (M = 2883.19ms, SE = 327.2) than older participants (M = 6295.39ms, SE = 342.4).

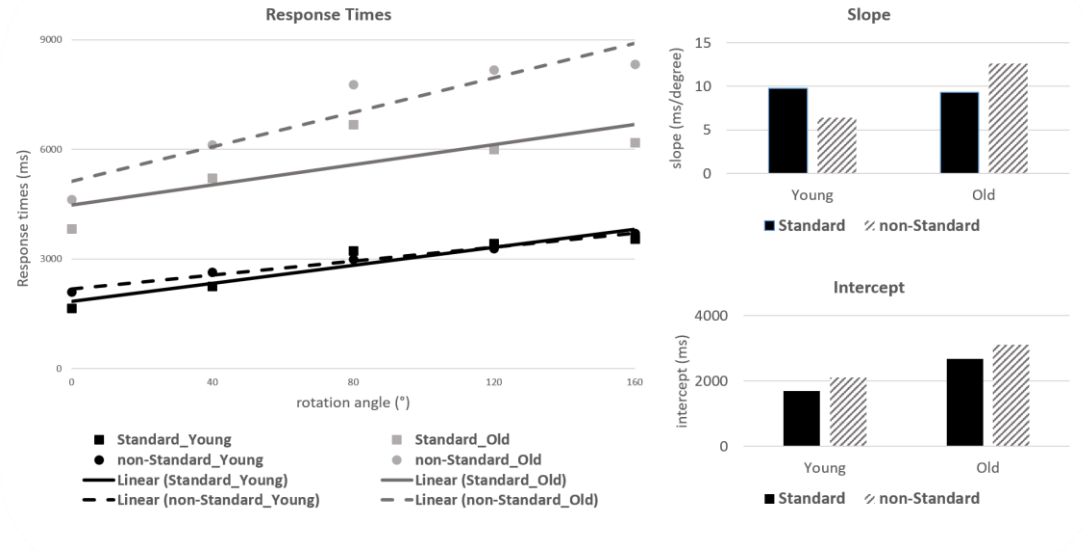

Figure 4-2. Younger and older participants' performance in in Standard (black) and non-Standard (grey) cube rotation in Experiment 4. The left panel reports the MR rate (slope) and the right panel depicts the intercept.

In addition, age was found to interact with stimulus complexity, F (1, 42) = 10.25, $p = .003$, $\eta^2 = .20$. Separate ANOVAs carried out for each age group revealed an effect of stimulus complexity in the older participants, F (1, 20) = 17.99, $p < .001$, $\eta^2 = .47$, with longer RTs observed for non-Standard objects (M = 7009.29ms, SE = 513.7) as compared to Standard ones (M = 5581.48ms, SE = 472.3). No such effect of stimulus complexity was found in younger participants, F (1, 22) = .23, $p = .64$, $\eta^2 = .01$. The three-way interaction between age, rotation angle and stimulus complexity was not statistically significant, F (3.3, 138.2) = 2.97, $p = .09$.

4.1.3.3 Slope and intercept

A main effect of age was observed on the estimated slope, F (1, 42) = 6.58, p = .014, η^2 = .14 (see Figure 4-2, top right panel). MR rates were significantly slower in older (M = 10.95ms/degree, SE = .8) than younger participants (M = 8.07ms/degree, SE = .8). In addition, age was found to interact with the stimulus complexity on the estimated slope measure, F (1, 42) = 16.29, $p < .001$, η^2 = .28. Follow-up comparisons carried out separately for Standard and non-Standard stimuli revealed that younger and older participants performed similarly in the Standard condition, t (42) = .30, p_c = .762, but differed significantly in processing the non-Standard stimuli, t (26.8) = -5.00, $p_c < .001$.

To further explore the strategy adopted by different age group, additional comparisons were carried out separately for younger and older participants. An effect of stimulus complexity on the slopes was revealed in both groups (younger: t (22) = 6.21, p_c = .021; older: t (20) = 13.73, p_c = .001). As shown in the top right panel of Figure 4-2, older participants were slower in rotating the non-Standard stimuli (M = 12.60ms/degree, SE = .82) compared to the Standard ones (M = 9.30ms/degree, SE = 1.08). By contrast, younger participants were faster in mentally rotating non-Standard (M = 6.39ms/degree, SE = .92) as compared to Standard stimuli (M = 9.76ms/degree, SE = 1.1).

In the estimated intercept measure (see Figure 4-2, bottom right panel), a main effect of stimulus complexity was found, F (1, 42) = 6.19, p = .017, η^2 = .13. A

larger intercept was observed in the non-Standard objects (M = 2610.01ms, SE = 196.8) than in the Standard ones (M = 2190.67ms, SE = 159.22). In addition, an ageing effect was observed in the intercept, F (1, 42) = 10.01, p = .003, η^2 = .19, with larger intercept for the older participants (M = 2899.96ms, SE = 228.3) as compared to the younger participants (M = 1900.73ms, SE = 218.2). However, no interaction between stimulus complexity and age group was found on the estimated intercept, F (1, 42) = .02, p = .97.

4.1.4 Discussion

No ageing effect was observed in MR rates when processing the relatively simpler Standard objects. However, a differential performance across age groups was observed when processing the non-Standard objects. Older participants showed a steeper slope in the non-Standard than in the Standard condition suggesting that they used piecemeal transformation in processing the more complex non-Standard objects. Younger participants adopted a holistic strategy while performing the MR task with Standard objects. The observation that their MR rates were faster in more complex non-Standard stimuli suggests that they simplified this task and transformed the partial image of these stimuli in their minds' eyes. This finding is consistent with the expected performance of higher VVI individuals who can automatically simplify the representation of non-Standard objects and transform such partial images in their minds' eyes as demonstrated by shallower slopes in the RTs function measured in the non-Standard as compared to the Standard condition.

Taken together, the results of the present experiment suggest that the different performance observed in younger and older participants can be explained by the different rotation strategies used by the two groups of participants.

4.2 Experiment 6

4.2.1 Introduction and brief recap

MR performance is strongly affected by the specific features of the stimuli that have to be mentally rotated. For example, more time is necessary to process 3D arm-like cube objects than 2D polygon stimuli (Shepard & Metzler, 1988). In the following experiment, we further explored the issue of strategy selection investigating whether the rotation strategy differences observed in Experiment 4 between younger and older participants could be generalised to different types of stimuli (i.e. 2D polygons). In this experiment, the complexity level of the polygons was manipulated through systematic changes to their number of vertices in line with earlier works on 2D polygons (Cooper, 1975; Coop & Podgorny, 1976).

4.2.2 Method

4.2.2.1 Participants

Another 20 younger (19 to 24 years old, mean $=$ 21.2 years old, 10 females) and 20 older participants (66 to 84 years old, mean $=$ 71.3 years old, 10 females) were recruited for this experiment. All younger and older participants were given the VVIQ-

2 (Marks, 1995). The VVIQ-2 scores were comparable between younger (mean = 129.7, SD = 14.0, range: 106-160) and older participants (mean = 130.75, SD = 11.8, range: 115-152), t (38) = -.26, p = .80. For both age groups, the lowest VVIQ-2 score was around 3 per item (younger = 3.3; older = 3.6). This means that for both younger and older participants rated their imaged scenes or items as moderately clear and vivid (see Appendix A for reference). Hence, we did not consider the scores of the VVIQ-2 as a factor in the data analyses.

4.2.2.2 Stimuli

Polygons were selected as the stimuli for the present experiment. To be consistent with Experiment 5, two types of stimuli were used, Standard and non-Standard (Figure 4-3). The Standard stimuli were integrated polygons with twelve vertices. The non-Standard stimuli were generated by dividing the Standard objects into three segments. Accordingly, the non-Standard objects still contain twelve vertices but consist of three separate segments.

On each trial a pair of objects was presented with a different orientation, from 0°, 60° to 120° (three rotation angle) clockwise or counter-clockwise (two orientations of rotation). Half of the trials was set as a pair of normal objects and the other half was set as a pair of mirrored objects. In each block, both normal and mirror pairs were randomly presented with five repetitions. In total two blocks of 120 trials were presented separately for Standard and non-Standard stimuli. The order with which

these two blocks were presented was counterbalanced across participants in each ageing group.

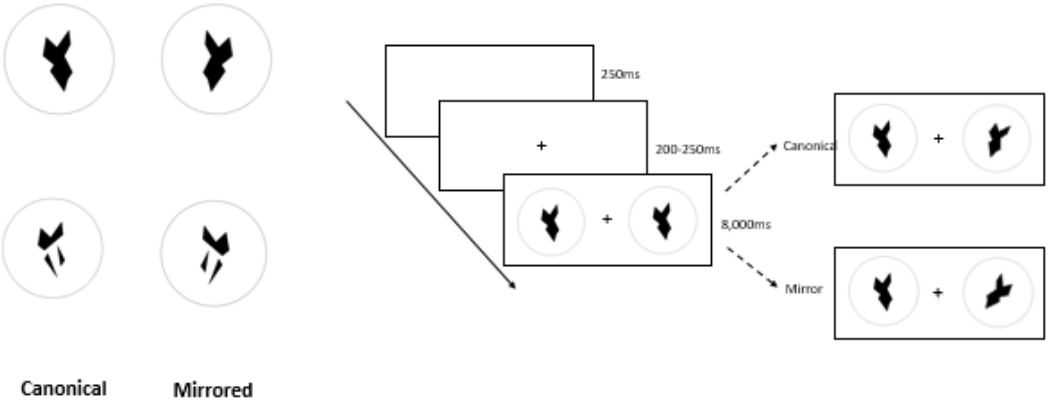

Figure 4-3. The stimuli and experimental procedure used in polygon rotation (Experiment 5). The left panel presents two types of canonical stimuli and their corresponding mirror images. The top row presents the Standard objects and the bottom row presents the non-Standard objects. The right panel presents the experimental procedure in polygon rotation task.

4.2.2.3 Procedure

The procedure of Experiment 6 is shown in the right panel of Figure 4-3. Each trial began with a white screen presented for 250ms, followed by a fixation cross (black on white background) lasting for a randomly selected interval between 200ms and 250ms, then a pair of polygon stimuli was presented for a maximum of 4,000ms or until a response was given by the participant. In case of missed responses, a new trial was presented. Participants had to indicate whether these two polygons were the same (normal though rotated) or different images (mirror) by pressing the “S” or “D” buttons.

During the whole procedure, the participants were asked to keep their hands on the keyboard.

A run-in of 15 trials served as practice allowing participants to familiarize with the task. In this practice session, two different 12-vertices polygons (Standard and non-Standard) not used in the following experimental blocks were generated and used to avoid practice effect.

4.2.2.4 Data analysis

The data analysis was identical to that performed in Experiment 4.

4.2.3 Results

4.2.3.1 Accuracy

A significant main effect of rotation angle was observed, F (2, 76) $=$ 40.12, p $<$ .001, $\eta^2 =$ .51. The accuracy rate linearly decreased with rotation angle, F (1, 38) $=$ 66.73, p $<$ .001. No main effect of stimulus complexity, F (1, 38) $=$ .01, p $=$ .968, and no interaction between stimulus complexity and rotation angle, F (2, 76) $=$ .13, p $=$ .877, were found in the accuracy rates.

A significant main effect of age, F (1, 38) $=$ 21.38, p $<$ .001, $\eta^2 =$ .36, revealed that younger participants were more accurate (M $=$ 91.3%, SE $=$ 2.7) than older participants (M $=$ 73.4%, SE $=$ 2.7). The factor age did not interact with stimulus complexity, F (1, 38) $=$ .20, p $=$ .657. In addition, no significant age $\times$ stimulus complexity $\times$ rotation angle was observed, F (2, 76) $=$ 1.88, p $=$ .160.

4.2.3.2 Response Times

The performance across younger and older participants is summarised in Figure 4-4. Consistently with previous literature (Shepard & Metzler, 1971), a main effect of rotation angle was observed in RTs, F (2, 76) = 156.92, $p < .001$, $\eta^2 = .81$, which was confirmed fit for a linear trend, F (1, 38) = 228.80, $p < .001$, $\eta^2 = .86$. In addition, the main effect of stimulus complexity, F (1, 38) = 5.31, $p = .027$, $\eta^2 = .12$, revealed longer RTs for Standard objects (M = 2043.4ms, SE = 56.4) than non-Standard ones (M = 1887.3ms, SE = 52.0). However, no interaction between stimulus complexity and rotation angle was found, F (2, 76) = .49, $p = .612$.

Consistent with the outcome of Experiment 4, an age-associated delay was found, F (1, 38) = 110.97, $p < .001$, $\eta^2 = .75$. Older participants showed longer RTs (M = 2411.7ms, SE = 59.9) than younger ones (M = 1519.1ms, SE = 59.9). However, age was not observed interacted with other factors (age × stimulus complexity, F (1, 38) = 1.25, $p = .271$; age × rotation angle, F (2, 76) = 2.26, $p = .07$; age × stimulus complexity × rotation angle, F (2, 76) = 2.20, $p = .118$).

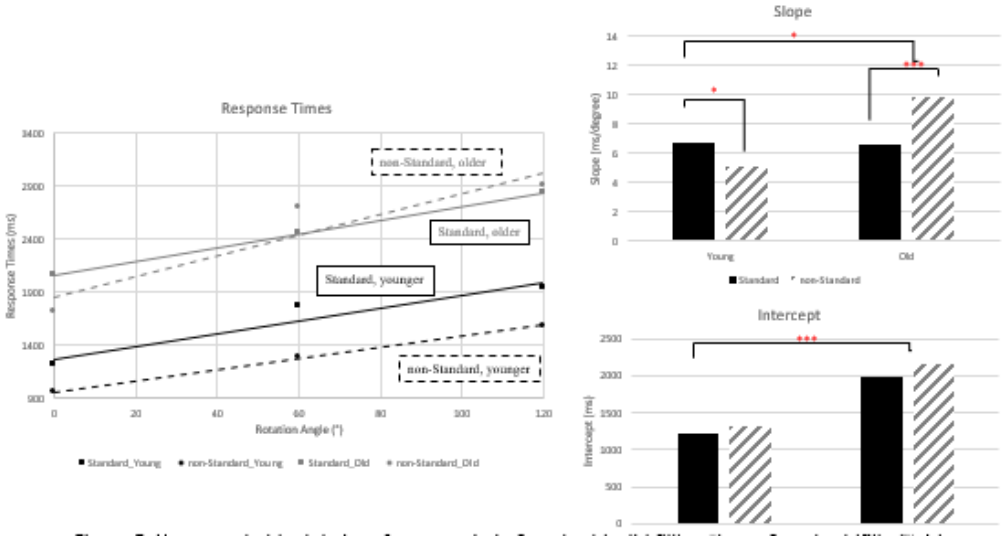

Figure 4-4. Younger and older participants' performance in in Standard (solid fill) and non-Standard (filled with upward diagonal) polygon object rotation in Experiment 5. The left panel presents the MR rate (slope) and the right panel presents the intercept.

4.3.3.3 Slope and Intercept

As shown in the top right panel of Figure 4-4, a main effect of age was observed in the estimated slope in RTs function, F (1, 38) = 8.14, p = .007, η^2 = .18. Older participants' performance was slower (M = 8.21ms/degree, SE = .56) than younger participants' one (M = 5.9ms/degree, SE = .6).

Moreover, age was found to interact with stimulus complexity, F (1, 38) = 37.38, p < .001, η^2 = .50. Follow-up analyses carried out separately for standard and non-standard objects revealed that there was no age-associated difference in processing Standard objects, t (38) = .17, p_c = .867. However, MR rates for non-Standard objects were significantly slower in older (M = 9.8ms/degree, SE = .7)

than in younger participants (M = 5.1ms/degree, SE = .4), t (38) = -5.43, $p_c < .001$. Furthermore, additional pairwise comparisons were carried out on the estimated slopes measured for standard and non-standard stimuli separately for each age group. A significant main effect of stimulus complexity was observed in younger participants, t (19) = 3.41, $p_c = .018$, indicating that they were faster in processing non-Standard (M = 5.1ms/degree, SE = .4) than Standard objects (M = 6.8ms/degree, SE = .5). A main effect of stimulus complexity was also observed in the older group, t (19) = 31.11, $p_c < .001$. Here, it reflected the fact that older participants took longer to process non-Standard objects (M = 9.8ms/degree, SE = .7) as compared to Standard ones (M = 6.6ms/degree, SE = .8).

The intercepts in RTs functions in younger and older participants are depicted on the bottom right panel of Figure 4-4. A main effect of age was found on the estimated intercept, F (1, 38) = 64.73, $p < .001$, $\eta^2 = .63$, with a larger intercept observed for older (M = 2063.7ms, SE = 69.8) than younger participants (M = 1269.2ms, SE = 69.8). However, age was not observed to interact with stimulus complexity, F (1, 38) = .44, $p = .513$.

4.2.4 Discussion

Similar to the performance observed in Experiment 4 during the rotation of 3D objects, systematic age-related differences were observed in the MR rate of 2D polygon stimuli. More specifically, while no difference between younger and older individuals was present for the MR rate of Standard stimuli, older participants showed

significantly slower rotation rates than the younger while transforming the more complex non-Standard stimuli. The presence of stimulus complexity effects in each age group revealed that both younger and older participants adopted different strategies in processing 2D polygons with different complexity levels. However, while older participants showed steeper MR rates for the multi-part non-Standard polygons as compared to the simpler Standard ones, younger participants had faster MR rates for the more complex non-Standard polygon stimuli than for the Standard ones.

The similar pattern of results related to the rotation rates of 3D (Experiment 4) and 2D (Experiment 5) objects suggests that the dimensionality of the visual stimuli does not affect the strategy selection adopted by younger and older individuals during the mental rotation of unfamiliar objects.

4.3 General Discussion for Experiment 5 and Experiment 6

Younger and older participants performed two MR tasks with different types of unfamiliar objects, 3D cube stimuli (Experiment 4) and 2D polygons (Experiment 5). In both experiments stimulus complexity was manipulated by increasing the number of segments that constituted each object. Non-Standard stimuli were characterized by higher complexity as compared to Standard ones (three segments vs. one segment, respectively). As expected, the analysis of both RTs and accuracy rates showed the presence of a complexity effect with faster response time and increased

accuracy observed for Standard than non-Standard visual stimuli regardless of age (Bethell-Fox & Shepard, 1988; Heil & Jansen-Osmann, 2008).

Consistent with previous literature (e.g., Band & Kok, 2000; Borella et al., 2014), an age-associated delay in RTs was found during the mental rotation of unfamiliar objects in both experiments of the present study. This general age related difference was further supported by the analysis of the estimated intercepts and slopes calculated by inserting a linear line into each participant's RTs as a function of rotation angle. A larger intercept was observed during the mental rotation of both polygons (Experiment 5) and cubes (Experiment 4) in older than in younger participants. This result suggests that older adults are slower in the initial phase of stimuli encoding/identification or in the final decision making stage (or both), which is in line with previous observations (e.g., Dror & Kosslyn, 1994). In addition, as reported in other MR studies with unfamiliar objects (e.g., Hertzog & Pypma, 1991; Puglisi & Morrell, 1986), there was an effect of age on the slopes derived from the RTs functions: the MR rate was slower in older than younger adults for both the polygons and cubes rotation tasks.

To investigate whether different rotation strategies in different age groups could explain age-related differences in MR processing, we used the MR slopes measured for Standard and non-Standard objects as an indication of the strategy adopted during the mental rotation task. The age × stimulus complexity interactions observed for the slopes calculated in both Experiments 4 and 5 revealed systematic

differences between the MR rates of younger and older participants with stimuli of different complexities. During the mental rotation of simple (Standard) objects, MR rates were comparable across younger and older participants. This finding is consistent with the literature whereby the holistic strategy is considered as the default strategy commonly used in processing integrated objects (like Standard stimuli in the present study), familiar or unfamiliar, and regardless of participants' age (Dror et al., 2005; Khooshabeh et al., 2013). By contrast, an age-associated difference in MR rates was evident for the more complex (non-Standard) objects: older participants processed these objects more slowly than younger ones.

In addition, results showed the presence of a main effect of stimulus complexity on the slopes for both younger and older participants suggesting that participants with normal-to-good ability in VVI applied different strategies in MR tasks when stimuli of different complexity had to be rotated. However, while younger participants showed slower MR rates for simple than complex stimuli, an opposite pattern of results was observed for older participants with slower MR rates for complex as compared to simple objects. This suggests that different strategies were used by younger and older individuals during the rotation of Standard and non-Standard objects, as discussed below. Importantly, similar results were found in each age group during the mental rotation of both 3D cube objects (Experiment 4) and 2D polygon stimuli (Experiment 5).

For older participants, a steeper slope was observed in processing non-Standard objects than in processing Standard objects. According to the stimulus complexity hypothesis (Cooper, 1975), this result suggests that older participants transformed the multi-part non-Standard objects piece-by-piece rather than holistically. This finding is in striking contrast with that of Dror et al. (2005) who reported that older participants did not change their strategy as a function of stimulus complexity and maintained a holistic strategy to process both simple and complex objects. These inconsistent findings may be accounted for in terms of stimulus familiarity. Dror et al. (2005) used familiar objects whereas in the present experiment we used unfamiliar polygons and arm-like cube objects. The holistic strategy is more likely to be used when the stimuli are familiar or over-learned (Bethell-Fox & Roger, 1988) as these representations are already stored in memory. Older participants might have no difficulty in creating the representation of such familiar objects even when these are more complex and they can therefore rotate the whole image to complete the task. By contrast, additional cognitive resources might be needed to mentally represent unfamiliar objects as compared to familiar ones. In the present study, in which unfamiliar stimuli posed high cognitive demands, older participants adopted the same holistic strategy as younger individuals to complete the rotation of simple integrated (Standard) objects. However, they used a piece-by-piece strategy to rotate complex non-standard objects. Given their deficits in feature binding in working memory (Chalfonte & Johnson, 1996; Mitchell, Johnson, Raye, & D'Esposito, 2000), it is possible that older participants encountered

selective difficulties in representing the multi-part (non-Standard) unfamiliar objects as a unit and therefore had to use a piece-by-piece strategy to complete the tasks, despite the higher cognitive demands posed by this strategy.

The younger participants in the present experiment showed a shallower slope in processing non-Standard than in processing Standard objects. This result resonates with the higher VVI individuals' performance in Experiment 4 as well as other results one could glean from the literature (Yuille & Steiger, 1982). It suggests that younger participants, at least those who have normal-to-good level of VVI, may simplify the representation of the multi-part non-Standard stimuli and maintain such simplified image for further mental manipulation (Liesefeld & Zimmer, 2013). This explanation indeed corresponds to our participants' comments in the debriefing session. Most of the younger participants (18 out of 19 in Experiment 4 and 18 out of 20 in Experiment 5) reported focusing on the main body (see details in Figure 4-1 & Figure 4-3) and one of the two small segments only. Thus, consistent with existing literature these findings demonstrate that younger individuals with normal-to-good VVI have the ability to simplify their representation of the visual stimuli then rotate this in their minds' eyes.

An alternative explanation for this age difference in MR rate could be that older were more cautious with more complex non-Standard stimuli than younger individuals, hence produced a steeper slope in RTs function of rotation angle. If this were the case older participants should be proportionally more accurate in larger rotation angles in the more complex non-Standard condition as compared to younger adults. However,

no three-way interaction was observed among age, rotation angle and stimulus complexity in accuracy rate in either experiment, therefore not supporting this alternative account.

All in all, these results suggest that age affects the strategy selection in MR process with unfamiliar objects, especially when the objects consist of multiple parts. In processing unfamiliar integrated objects, older participants did not show differential MR rates compared to younger participants. However, during the MR of multi-part objects, older participants were not as proficient as younger participants in maintaining precise object representations for the MR processing. Instead, they transformed the multi-part objects piece by piece to comply with the requirements of the MR task. The use of a different strategy at an older age provides an explanation for the slower MR rates observed in older participants.

4.4 Experiment 7

4.4.1 Brief introduction

Except of the slowing in the MR rate, the analysis of the RTs functions consistently shows the presence of a larger intercept in RTs function of rotation angle for older as compared to younger individuals (Dror & Kosslyn, 1994; Saimpont et al.,

2009; Thomas, 2016). The intercept represents the speed of responses in two distinct cognitive processes, the identification of the stimuli and the execution of the responses (Cooper & Shepard, 1973; Just & Carpenter, 1976). Thus, it remains unclear which of these two cognitive processes involved in a MR task are affected by ageing. The presence of an age-associated slowing in motor-response generation has been well documented in the literature (Falkenstein, Yordanova, Kolev, 2006; Roggeveen, Prime & Ward, 2007). It is therefore likely that the selection and execution of the correct response after stimulus rotation takes longer in older than younger adults in MR tasks. However, it is possible that in addition to the age related slowing of response selection and execution, older adults are slower during the initial stimulus encoding phase before the onset of MR.

Electrophysiological measures have been used to characterise the time course of the process associated with MR. ERP studies investigating the neural mechanism of MR have primarily used familiar stimuli (e.g. letters or digits). The analyses of ERPs elicited by both standard and mirror stimuli have shown the presence of a slow negative-going ERP component between 350 and 650ms post-stimulus onset, the so called rotation related negativity (RRN), which is maximal over parietal electrodes and sensitive to the rotation angle of the stimuli (e.g. Núñez-Peña & Aznar-Casanova, 2009; Núñez-Peña, Aznar, Linares, Corral, & Escera, 2005, Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989). Specifically, the amplitude of this ERP component becomes more negative with increased rotation angles (for a review see

Heil, 2002). Over the past 30 years, the RRN has been used as a tool to investigate the cognitive processes underlying MR. For example, the onset of the RRN was found to be delayed when the perceptual quality of the stimulus was deteriorated or when the stimulus was more difficult to discriminate (e.g., Heil and Rolke, 2002). Thus, when the initial encoding phase took longer, the onset of the RNN was delayed. Therefore, they suggested that the onset of RRN could be used as a temporal marker for the onset of the pure MR process.

To explicate the ageing effects in specific sub-processes in MR, we compared directly the time course of the MR processes in younger and older individuals. Electrophysiological and behavioural measures were collected during a classic letter rotation task (e.g. Hamm, Johnson & Corballis, 2004; Heil, 2002) in which participants reported the normal or mirrored version of the character presented on the screen. If older adults are slower than younger participants in encoding the stimuli during the initial processing stage, the following stage - mental rotation proper - should be delayed in this age group. This should be observed in both behavioural and ERP measures and specifically reflected by larger intercepts in the RT function of rotation angles as well as an age-associated delay in the onset of the RRN for older than younger participants.

4.4.2 Method

4.4.2.1 Participants

Twenty-six younger (13 women; age 18-29 years, mean = 21.0, standard deviation = 2.9) and twenty-six older adults (13 women; age 66-79 years, mean = 73.6, standard deviation = 4.5) were recruited in this experiment. All of them reported no history of neurological disorders and gave written informed consent to participate in the study after the nature of the study had been explained to them.

4.4.2.2. Stimuli and procedure

Participants were seated in an electrically shielded, dimly lit, sound attenuating room. The computer monitor was located at a distance of 76cm in front of the participants, whose eyes were aligned with the monitor centre. Upper character letters (F, L, P and R) were used as stimuli in this study. The letters presented in white on a black background (height: 3 cm, 2.26° of visual angle). These letters were presented in a canonical way (normal letter) or flipped according to their vertical meridian (mirror letter). On different trials these stimuli were presented at different orientations with a rotation angle of 0°, 30°, 60°, 90°, 120° and 150° (6 rotation angles). Stimulus rotation followed two different directions clockwise or counter-clockwise from the vertical upright position of the stimuli.

Each trial began with a white fixation cross (1cm × 1cm) presented at the centre of a black background for 100ms. This was followed by a letter presented at the screen centre for 500ms, after which a fixation cross remained on the screen for a variable interval randomly selected between 1,800 and 2,100ms. Participants were instructed to respond as fast and as accurately as possible to determine whether the

letter on the screen was presented as normal or mirrored version. Each block included 96 trials (4 letters × 2 stimulus type × 6 rotation angle × 2 orientation of the rotation) presented in random order. Each participant completed ten blocks.

During EEG recording, participants were instructed to keep their eyes on the fixation presented on the screen and their index fingers on the two keys on the response box, which was vertically arranged in front of them. The top button was set for responses to normal stimuli and the bottom was set for responses to mirror stimuli. While the stimulus to response key mapping was held constant throughout the experiment, the responding hand to response key mapping (left hand on the top key and right hand on the bottom key) was changed after each block. Before the experiment began, participants completed a training block of 48 trials to familiarise with this MR task. Here, the letters "G" and "J" were used which were not included in the set of experimental stimuli.

After the MR task, all participants were asked to fill in the VVIQ-2 (Marks, 1995; see Appendix A).

4.4.2.3 Recording and Data Analysis

Electrophysiological recording and analysis

EEG was recorded from 70 active electrodes (BioSemi Active Two system). Horizontal EOG (hEOG) was recorded unipolarly from the outer canthi of both eyes and vertical EOG (vEOG) was recorded bipolarly both vertically from above and below the right eye. The impedances of the earlobe reference electrodes were kept as

equal as possible. Amplifier band pass was 0.53–40 Hz, and digitisation rate was 512 Hz. EEG, hEOG and vEOG were segmented into 750ms long epochs starting from 100ms before stimulus onset. Trials with eye blinks (VEOG exceeding $\pm$ 60 μV), horizontal eye movements (HEOG exceeding $\pm$ 80 μV), or other artefacts (a voltage at any scalp site exceeding $\pm$ 80 μV) throughout the epoch were excluded from analysis.

Statistical analyses were conducted on the basis of ERP mean amplitudes obtained at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) within three consecutive measurement windows 200-350ms, 350-500ms and 500-650ms. Separate analyses were run for ERPs triggered by visual stimuli in each time window. Separate averages were computed for normal and mirror letters, and for different rotation angles (0°, 30°, 60°, 90°, 120° and 150°). The data from the same rotation angle clockwise and counter-clockwise were combined. Consistent with existing literature (Kartzman & Terry, 1983; Picton, Stuss, Champagne & Nelson, 1984), ERP amplitudes were smaller in older as compared to younger participants (a main effect of age was evident in the 200-350ms, 350-500ms and 500-650ms time windows - all *F*s (1, 48) $\geq$ 5.38, all *p*s $\leq$ .025, all $\eta^2 \geq .10$). This amplitude difference between the younger and older individuals may represent some physical difference in skull-thickness (Picton et al., 1984). Thus, to avoid possible confounds driven by this general ERP difference across groups, ERP analyses were carried out directly on the amplitudes of the RRN components calculated by subtracting ERPs elicited on the non-rotation trials (0°) from

ERPs elicited on different rotation angles trials (30°, 60°, 90°, 120°, 150°) in the corresponding conditions. Grand-averages of these difference waves were analysed with mixed ANOVAs with age (younger or older) as between-subject factor as well as stimulus type (normal or mirror) and rotation angle (30°, 60°, 90°, 120°, 150°) as within-subject factors[12]. Because the RRN component was only detected between 350-650ms after stimuli onset, ERP results will be reported exclusively for these time windows (350-500ms and 500-650ms).

Because our main variable of interest was rotation angle, interactions involving rotation angle were followed-up with further ANOVAs and trend analyses to investigate the presence and characteristic of rotation angle under different experimental conditions or in different groups.

Behavioural analysis

In all the analyses presented below, the data from the same orientation clockwise and counter-clockwise were combined. RTs exceeding two standard deviations above or below the mean calculated separately for each experimental condition and each subject were excluded (4.8% of the trials on average). Mixed ANOVAs were carried out on both mean accuracy rates and mean response times (RTs,

[12] The VVIQ performance was comparable between younger (mean = 128.7, SD = 20.5, range: 84- 160) and older adults (mean = 131.8, SD = 13.7, range: 115- 153), $t(50) = -.63$, $p = .53$. Moreover, the VVIQ-2 score was normally distributed in younger (Shapiro-Wilk test: $p = .153$) but not in older participants (Shapiro-Wilk test: $p = .003$). Therefore, we did not consider VVIQ-2 scores as a factor in the main data analyses.

calculated over correct trials only) with stimulus type (normal or mirror) and rotation angle (0°, 30°, 60°, 90°, 120°, 150°) as within-subject factors and age (younger or older) as between-subject factor[13]. To fully characterise the cognitive processes underlying MR, whenever significant main effects or interactions involving the factor rotation angle were observed, linear regression analyses were carried out to calculate the estimated slopes and intercepts in the RTs as a function of rotation angle. In these cases, additional ANOVAs were carried out on the estimated slopes and intercepts to further investigate the rate of MR or the time needed to encode stimuli and to respond, respectively, for different stimulus types or in different age groups.

4.4.3 Behavioural Results

4.4.3.1 Response Times

The RT analysis revealed a main effect of rotation angle, $F\ (1.6,\ 81.4) = 250.98, p < .001, \eta^2 = .83$. RTs linearly increased with increasing rotation angles, $F\ (1,\ 50) = 325.69, p < .001, \eta^2 = .78$. In addition, there was a main effect of stimulus type, $F\ (1,\ 50) = 200.17, p < .001, \eta^2 = .80$, with longer RTs in the mirror condition

[13] Preliminary analyses including the factor gender revealed no effect of gender in the behavioural results. In the ERPs data analyses, ERPs measured in women were more negative than those measured in man regardless of their age as revealed by a main effect of gender observed between 350 and 650ms post-stimuli (both *p*s $\leq$ .019). However, the factor gender did not interact with any other factor, all *p-values* $>$.05. Thus, the factor gender was not included in the final analyses.

(M = 836.6ms, SD = 199.2) as compared to the normal one (M = 720ms, SD = 157). The ANOVA also yielded a significant stimulus type × rotation angle interaction, F (2.7, 133.8) = 7.30, $p < .001$, $\eta^2 = .13$. Separate analyses carried out for each stimulus type showed significant main effects of rotation angle for both normal (F (1.7, 87.1) = 261.62, $p < .001$, $\eta^2 = .84$) and mirror letters (F (2.0, 100.8) = 121.50, $p < .001$, $\eta^2 = .71$). RTs and rotation angles were linearly related in both cases (both Fs ≥ 166.61, ps < .001, $\eta^2 \geq .77$). As shown in Figure 4-5, the rate of mental rotation (slope) was slower for mirror letters (mean = 1.7ms/degree, SD = 0.8) than normal ones (mean = 2.0ms/degree, SD = 0.9), F (1, 50) = 4.18, p = .046, η^2 = .08. Furthermore, a larger intercept, F (1, 50) = 88.12, $p < .001$, $\eta^2 = .63$, was present for mirror (mean = 579.6ms, SD = 178.1) than normal letters (mean = 712.9ms, SD = 123.2).

The main effect of age, F (1, 50) = 39.71, $p < .001$, $\eta^2 = .44$, revealed that younger (mean = 662.3ms, SD = 131.3) were faster than the older adults (mean = 894.4ms, SD = 145.4) in this letter MR task. In addition, the interaction between age and stimulus type emerged to be significant, F (1, 50) = 16.28, $p < .001$, $\eta^2 = .25$. Follow-up analyses were conducted separately for each stimulus type. Main effects of age were present during the mental rotation of both normal (F (1, 50) = 33.58, $p < .001$, $\eta^2 = .40$, younger = 620.6ms, SD = 84.4; older = 819.5ms, SD = 131.9) and mirror stimuli (F (1, 50) = 41.19, $p < .001$, $\eta^2 = .45$, younger = 704.0ms, SD = 75.9; older = 969.2ms, SD = 111.0). This suggests that although reliable

differences between age groups were present for both stimulus types, these were more pronounced for mirror stimuli.

The ANOVA also revealed a significant interaction between age and rotation angle, F (1.6, 81.4) = 11.81, $p < .001$, $\eta^2 = .19$. The main effect of rotation angle which was present in both younger (F (1.5, 38.2) = 108.06, $p < .001$, $\eta^2 = .81$) and older participants (F (1.6, 41.1) =144.68, $p < .001$, $\eta^2 = .85$). A linear increase in RTs with rotation angles was observed in each age group (both Fs ≥ 158.48, ps < .001, $\eta^2 \geq .86$). Additional analyses revealed that the MR rate was slower in older participants as compared to younger ones (older: M = 2.1ms/degree, SD = 0.8; younger: M = 1.4ms/degree, SD = 0.6), t (50) = -3.82, $p < .001$. In addition, a larger intercept was observed in the older than in the younger (older: M = 725.3ms, SD = 133.1; young: M = 567.2ms, SD = 108.5), t (50) = -4.69, $p < .001$, suggesting that older individuals spent more time either encoding the stimuli or making decisions.

No other main effect or interaction was statistically significant. However, as we aimed to explore the performance of younger and older adults in MR in each experimental condition, the intercept of RTs function was further analysed by applying mixed ANOVAs with stimulus type (normal vs. mirror) as a within-subject factor and age (younger vs. older) as a between-subject factor. An interaction of age and stimulus type was found on the intercept, F (1, 50) = 8.37, p =.006. Main effects of age were present in both normal (t (50) = -4.788, $p < .001$) and mirror conditions (t (50) = -

5.493, $p < .001$). In normal condition, older adults (M = 647.43ms, SE = 20.7) spent about 140ms longer RTs in the non-rotation process as compared to the younger (M = 507.32ms, SE = 20.7), whereas the older (M = 821.51ms SE = 27.9) induced around 220ms longer RTs in mirror condition as compared to younger participants (M = 604.69ms, SE = 27.9).

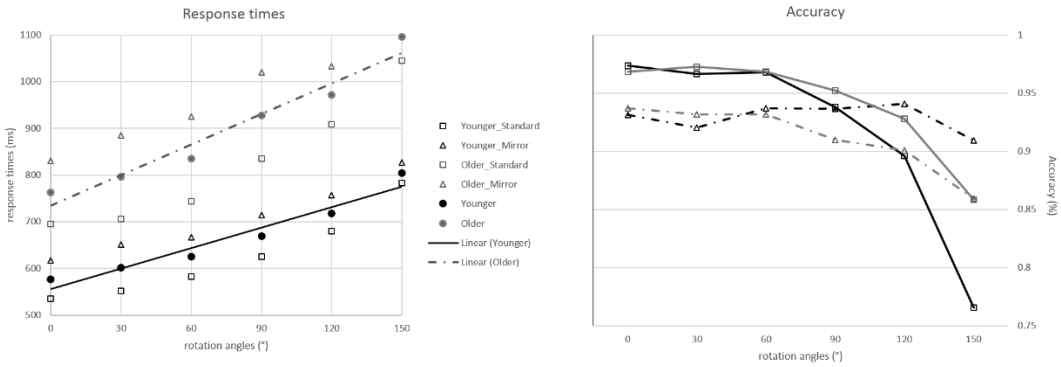

Figure 4-5. Behavioural performance in letter rotation task for younger and older adults. The left panel depicted the response times for both younger and older adult and the right panel depicted their accuracy rate in all rotation angles.

4.4.3.2 Accuracy

A main effect of rotation angle was observed on the accuracy rates, F (1.8, 89.6) $= 56.67$, $p < .001$, $\eta^2 = .53$, while no effect of stimulus type was present, F (1, 50) $= 1.23$, $p = .273$, $\eta^2 = .02$. Accuracy rate decreased with increasing rotation angles (linear trend analysis: F (1, 50) = 71.53, $p < .001$, $\eta^2 = .59$). The ANOVA also yielded a stimulus type $\times$ rotation angle interaction, F (1.3, 64.0) $= 9.29$, $p = .002$, $\eta^2 = .16$. Follow-up analyses conducted separately for each stimulus type revealed that the effects of rotation angle were present for both the normal (F (1.3, 63.1) $= 38.42$, p

$< .001$, $\eta^2 = .44$) and the mirror letter (F (1.6, 78.1) $= 6.11$, $p = .007$, $\eta^2 = .23$). In both cases, the linear relationship of RTs and rotation angle was confirmed (Fs $\geq$ 35.06, ps $\leq .011$, $\eta^2 \leq .58$). The decreasing rate of accuracy with increasing rotation angles was significantly faster in the normal (mean = -0.1%/degree, SD = 0.1) than in the mirror condition (mean = -0.2%/degree, SD = 0.1), F (1, 50) = 6.25, p = .016.

There was no main effect of age on accuracy, F (1, 50) = .09, $p > .05$. However, age was found to interact with stimulus type, F (1, 50) = 7.45, p = .009, η^2 = .13. Follow-up analyses conducted separately for each age group revealed that the older were more accurate to respond to normal letters (mean= 94.2%, SD= 5.2) than mirror ones (mean = 90.9%, SD = 9.7), F (1, 25) = 7.36, p = .040, η^2 = .16, but no such difference was found in younger adults, F (1, 25) = 3.06, $p > .05$, η^2 = .11.

Moreover, a three-way interaction between stimulus type, rotation angle and age was found on accuracy rate, F (1.3, 64.0) = 4.04, p = .039, η^2 = .08. Follow-up analyses were conducted separately for each stimulus version and revealed no interaction of age × rotation angle in both normal (F (1.3, 63.3) = 2.48, p = .113) and mirror conditions (F (1.6, 78.2) = 3.10, p = .063).

4.4.4 Event-related potentials

The RRN component was computed by subtracting the ERP waveforms elicited in the upright position (0°) from those elicited in each rotation angle (30°, 60°,

90°, 120°, 150°) separately for each participant and each stimulus type (normal vs. mirror).

Figure 4-6 shows the grand-average difference waveforms in each rotation angle for younger and older groups (top and bottom left panels, respectively) pooled over central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4). The RRN components elicited during MR of normal and mirror letters are shown in the central and right panels, respectively, separately for younger (top) and older (bottom) individuals. A general age-associated delay is visible in all these figures. While RRN amplitudes appeared to be modulated by rotation angle in both early (350-500ms) and late (500-650ms) time windows in younger participants, this RRN modulation by rotation angle was only visible in the late time window (500-650ms) in older participants, regardless of stimulus type.

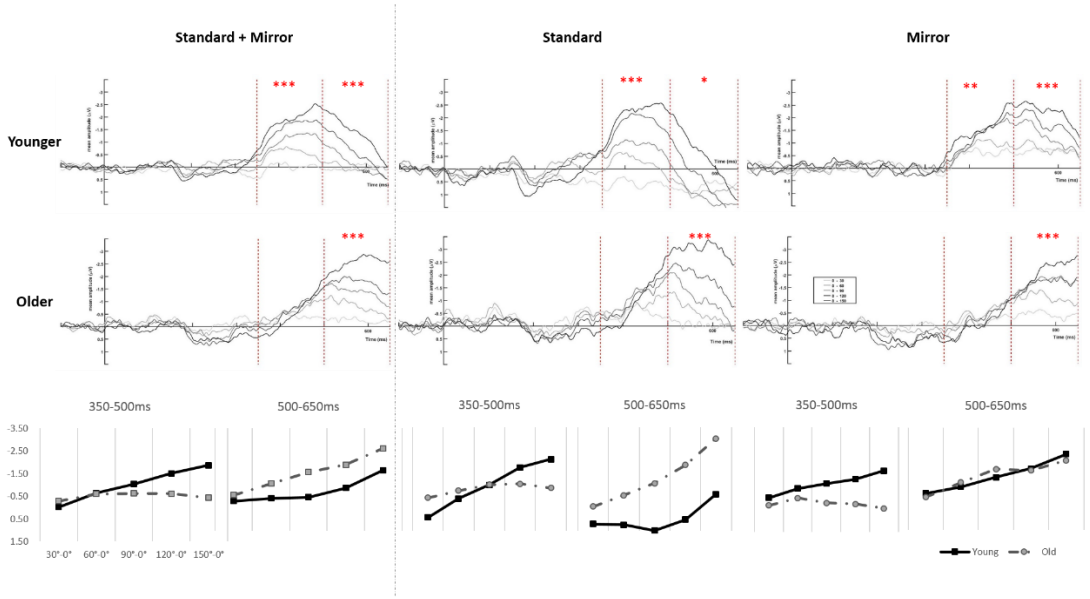

Figure 4-6. ERPs in younger (top row) and older adults (middle row) in normal (left panel in Figure 4-6b) and mirror (right panel in Figure 4-6b) as well as the average of

these two conditions (Figure 4-6a). The bottom row depicted the mean amplitude of ERPs for younger (solid line) and older adults (dotted line) in two consecutive time windows, 350-500ms and 500-650ms.

4.4.4.1 Early RRN time window (350-500ms)

A main effect of rotation angle was observed in this early RRN time window measured between 350 and 500ms post-stimulus onset (F (2.5, 123.5) = 19.98, p < .001, η^2 = .28). Linear trend analyses revealed that the RRN amplitude became more negative with the increasing rotation angles (F (1, 50) = 32.7, p < .001, η^2 = .39). In addition, stimulus type was found to interact with rotation angle, F (3.8, 188.5) = 10.10, p < .001. Repeated-measures ANOVA conducted separately for the different stimulus types revealed the presence of main effects of rotation angles for both normal (F (2.8, 138.4) = 27.88, p < .001, η^2 = .36) and mirror letters (F (3.3, 164.7) = 3.29, p = .012, η^2 = .06). RRN amplitude and rotation angles were linearly related in both normal (F (1, 50) = 51.34, p < .001, η^2 = .51) and mirror conditions (F (1, 50) = 6.30, p = .015, η^2 = .11).

The main effect of age, F (1, 50) = 4.02, p = .050, η^2 = .07, revealed that RRN amplitudes were larger in younger (M = -1.0, SE = 0.2) than older individuals (M = -0.5, SE = 0.2). Furthermore, differences between the RRN elicited in the normal and mirror letter conditions were observed between the two age groups as revealed by significant age × stimulus type interactions (Fs > 15.81, ps < .021, η^2 > .10). Follow-up analyses conducted separately for each stimulus type revealed

similar RRN amplitudes in younger and older age groups in the normal condition (no main effect of age , t (50) = .46, p = .651). By contrast, in the mirror condition, RRN amplitudes were more pronounced in younger (M = -1.1, SE = 0.9) than older adults (M = -0.2, SE = 0.8), t (50) = 3.37, p = .001.

In addition, age-related discrepancy was presence on RRN with rotation angle (see Figure 4-6a) as revealed by the age × rotation angle interaction, F (2.5, 123.5) = 14.28, $p < .001$, $\eta^2 = .22$. Separate analyses were carried out for each age group revealed the presence of a main effect of rotation angle in younger participants, F (2.2, 54.8) = 28.53, $p < .001$, $\eta^2 = .53$. Linear trend analyses in younger participants confirmed that the RRN amplitude became more negative with increasing rotation angles, F (1, 25) = 48.19, $p < .001$, $\eta^2 = .66$. By contrast, no main effect of rotation angle emerged in older participants between 350 and 500ms (F (2.2, 55.8) = 1.63, p = .20).

There was no significant interaction between age, stimulus type and rotation angle, F (4, 200) = 1.643, p = .165. However, to further investigate the pattern of RRN elicited in younger and older participants during the mental rotation of different stimulus types, follow up analyses were carried out separately for normal and mirror conditions. As can be seen in Figure 4-6b, significant age × rotation angle interactions were found for both the normal (F (2.8, 138.4) = 13.03, $p < .001$, $\eta^2 = .21$) and the mirror (F (3.3, 164.7) = 5.73, p = .001, $\eta^2 = .10$) conditions. In younger individuals, the main effect of rotation angle was present for both normal (F (2.5, 61.5) = 35.98,

$p < .001$, $\eta^2 = .59$) and mirror stimuli (F (2.9, 73.3) = 6.66, $p = .001$, $\eta^2 = .210$), and linear trend analyses revealed that the amplitude of the RRN became more negative with the increasing rotation angles (both F (1, 25) $\geq$ 13.71, $p \leq .001$, $\eta^2 \geq .35$), revealing that younger adults indeed showed their MR effort in both normal and mirror condition in this early RRN time window. By contrast, no main effect of rotation angle was observed in older adults, for normal or mirror letters (both Fs $<$ 2.37, both $p > .102$).

4.4.4.2 Late RRN time window (500-600ms)

Main effects of stimulus type (F (1, 50) = 19.31, $p < .001$, $\eta^2 = .28$) and rotation angle (F (1.9, 95.9) = 37.46, $p < .001$, $\eta^2 = .43$) were reliably present between 500 and 650 post-stimuli. RRN amplitudes were more negative in the mirror condition (M = -1.9, SE = 0.2) than in the normal one (M = -0.4, SE = 0.2) and became more negative with the increasing rotation angles (linear trend analysis: F (1, 50) = 54.28, $p < .001$, $\eta^2 = .521$).

Moreover, the interaction of rotation angle and stimulus type emerged to be significant, F (2.7, 134.1) = 3.27, $p = .028$, $\eta^2 = .061$. Similar to the observation in the early RRN time window (350-500ms), the presence of a rotation angle main effect was observed for both normal (F (2.8, 113.9) = 26.23, $p < .001$, $\eta^2 = .34$) and mirror letters (F (2.1, 103.1) = 20.2, $p < .001$, $\eta^2 = .288$). Trend analyses confirmed the linear relationship between RRN amplitude and rotation angles in both stimulus types (both Fs $\geq$ 31.32, ps $< .001$, $\eta^2 \geq .39$).

In this late RRN phase measured between 500 and 650ms post-stimulus, RRN amplitudes were larger for older (M = -1.3, SE = 0.2) as compared to younger adults (M = -0.5, SE = 0.2) (main effect of age, F (1, 50) = 8.64, p = .005, η^2 = .15).

In addition, a significant age × stimulus type interaction (F (1, 50) = 16.74, p < .001, η2 > .25) revealed that enhanced RRN amplitudes were present for older (M = -1.3, SE = 1.3) as compared to younger adults (M = 0.4, SE = 1.5) in the normal condition (main effect of age, t (50) = -4.5, p < .001), while no ageing effect on RRN amplitudes was observed when participants rotated mirrored stimuli, t (50) = -.05, p = .953.

Finally, a three-way interaction between age, rotation angle, and stimulus type was observed in this late time window (see Figure 4-6b), F (2.7, 134.1) = 4.29, p = .008, η^2 = .08. Follow-up analyses conducted separately for the different stimulus type conditions investigated the presence of age × rotation angle interactions. In the normal letter condition, an age × rotation angle interaction was present (F (2.3, 113.9) = 6.08, p = .006, η^2 = .20). In younger adults, a main effect of rotation angle (F (2.4, 60.0) = 6.51, p = .002, η^2 = .21) reflected the fact that the RRN amplitudes were significantly larger at 150º as compared to 120º (p = .002), while no difference emerged between any other two consecutive angles, all ps > .519. Trend analyses revealed that the RRN amplitudes measured in the younger could be described by a linear trend, F (1, 25) = 6.28, p = .019, η^2 = .20. A main effect of rotation angle was also present in older adults, F (1.9, 47.1) = 24.24, p < .001, η^2 = .50. The RRN

increased with increasing rotation angles (F (1, 25) = 40.33, $p < .001$, $\eta^2 = .62$), and significant differences between consecutive degrees were found between 90 º and 120 º, $p = .005$, and between 120 º and 150 º, $p = .012$. As shown in Figure 4-6b, younger adults had almost completed the rotation processes of these stimuli while older participants were still rotating normal stimuli between 500 and 650ms post-stimulus. By contrast, no age × rotation angle interaction was present in the mirror letter condition, F (2.1, 103.1) = 1.00, $p = .409$, $\eta^2 = .02$. For both younger and the older individuals, the RRN increased with the increasing rotation angle, F (2.1, 103.1) = 20.19, $p < .001$, $\eta^2 = .29$. As can be seen in Figure 4-6, both age groups were still rotating mirror letters during this late time window.

4.4.5 RRN onset

To test whether the onset of the pure MR process is delayed in older than younger adults, we directly compared the RRN onset times measured in younger and older adults. Following the procedure introduced by Heil and Rolke did (2002), the RRN was measured by subtracting ERPs elicited in the 30º condition from those elicited in the 150º condition. The onset of the resulting RRN measured between 250 and 650ms post stimulus was compared across groups following the jackknife-based method (Miller, Patterson, and Ulrich, 1998) in each condition. Independent t-test was applied and revealed a main effect of age on the onset of RRN, t (50) = 49.73, $p < .001$, confirming a systematic delay in MR processes for older as compared to

younger participants (older: M = 587.3ms, SE = 0.3; young: M = 492.3ms, SE = 0.3).

4.4.6 Discussion

In the present experiment, we measured the behavioural and ERP correlates of letters MR in healthy younger and older adults to evaluate possible age differences. The RRN component was computed by subtracting the ERP waveforms elicited in the upright position (0°) from those elicited in each rotation angle (30°, 60°, 90°, 120°, 150°) separately for each participant and each stimulus type. Because the RRN components measured in the two age groups were characterised by different time courses, with delayed onset in the older, their average amplitudes were measured in two consecutive time windows between 350-500ms and 500-650ms post-stimulus.

ERP studies of MR have shown that the amplitude of the RRN component increases with increasing rotation angles (Heil & Rolke, 2002; Núñez-Peña et al., 2005; see Heil, 2002, for review). In line with these observations, main effects of rotation angle were observed between 350 and 650ms post stimulus in the present study, confirming that the RRN amplitude increased with increasing rotation angles.

When the RRN components elicited in younger and older individuals were directly compared, systematic differences emerged between age groups. In younger participants, the amplitude of the RRN measured between 350 and 500ms post-stimulus (early RRN phase), increased linearly as a function of rotation angle (see Figure 4-6a, top panel). This suggests that younger individuals were mentally rotating

the stimuli during this time window. By contrast, in older participants, the amplitude of the RRN component was not modulated by rotation angle during the early (350-500ms), although this modulation became apparent in the late time window (500-650ms) (Figure 4-6a, bottom panel). This suggests that MR processes in older participants were delayed as compared to younger individuals. This possibility is further supported by the additional analysis of the RRN onset confirming a delay in the onset of the RRN component for older as compared to younger individuals, as well as by the behavioural analysis which revealed a larger intercept of the RT functions for older as compared to younger participants. Taken together these findings reveal that MR processes occurred later in older adults.

This age induced delay in mental rotation was present for both normal and mirror stimuli. The analysis of RRN amplitudes measured between 350 and 500ms post stimulus revealed that they increased linearly with increasing rotation angles for both normal and mirror letters in younger but not in older participants (as shown in Figure 4-6b), suggesting that older participants were not mentally rotating stimuli during the early phase of the RRN. Further evidence for the consistent age-associated delay for both normal and mirror stimuli came from the analysis of the intercepts in the behavioural RTs function which showed that age induced delays were present for both normal and mirror stimuli even if such age difference was more pronounced for mirror than normal stimuli.

Existing electrophysiological evidence has suggested that different mechanisms underlie the rotation of mirror and normal stimuli. Rotating mirror letters might be more difficult compared to the rotation of normal stimuli because an additional rotation in and out of picture plane is needed (Hamm et al., 2004; Nunez-Pena & Aznar-Casanova, 2009). Thus, the rotation of mirror stimuli might start later and take longer (Bajric, Rosler, Heil & Hennighaugen, 1999; Murray, 1997; Nunez-Pena et al, 2009). Results observed for younger individuals provide direct evidence for the hypothesis that the mental rotation of mirror stimuli is more demanding than that of normal ones (e.g. to rotate the internal representation not only within but also out of the x-y coordinate plane; Hamm et al., 2004; Nunez-Pena & Aznar-Casanova, 2009; Quan et al., 2017). In line with evidence suggesting that this additional "flip-over" sub-process occurs in the late phase of MR (Quan et al., 2017), we observed that younger individuals were engaged in mirror rotation processes during both early and late RRN time windows whereas normal stimulus rotation was almost completed after the early RRN time window. This indicates that the cognitive processes underlying MR of mirror stimuli took longer than those involved in normal stimuli rotations. However, it is worth noting that due to the slow responses of older individuals (and the presence of a large number of biological artefacts in the EEG data (e.g. blinks) in this late processing stage), it was not possible to measure the presence of the RRN beyond 650ms post stimulus. Thus, it was not possible to investigate the duration of MR of mirror stimuli in older participants and to determine whether it was impacted by ageing.

Overall, our results revealed the presence of a general age-related delay in the onset of MR processes. One possible explanation is that older adults need more time to encode/ identify the stimuli before they can start the MR process. Previous ERP studies have shown that MR processes are delayed either when the perceptual quality of the stimuli is reduced or the stimuli are more difficult to discriminate (Heil & Rolke, 2002). In the present study the stimulus remained on screen for 500ms. That is, the stimulus disappeared well before participants were able to identify its version (as suggested by their reaction times). Under these experimental conditions participants were forced to create a mental representation of the stimulus and to fully rely on it during the following processes of mental rotation and decision making. It is therefore possible that older participants took longer to create this mental representation. It has been shown that working memory plays a relevant role in the maintenance of the mental representation of the letter during the rotation process (Hyun & Luck, 2007) and that it decreases with age (Brockmole, Parra, Della Sala & Logie, 2008; De Beni & Palladino, 2004; Reuter-Lorenz & Sylvester, 2005; Zacks, Lynn & Li, 2000). Thus, older adults might be not as efficient as younger adults in creating the internal mental representation which is the initial step necessary for MR.

While this age-related difference could simply be explained by the extended time necessary to older participants to encode the visual stimulus, it is interesting to note that they started to mentally rotate the stimuli (as indexed by the onset of RRN) only after the stimulus disappeared from the screen. This observation might also

suggest that disengaging attention from the external visual stimulus on the screen and directing it internally towards its mental representation was more challenging for older than younger participants. Indeed, recent lines of evidence have demonstrated that older participants find it more challenging to inhibit distracting information as compared to younger participants (Hasher, Zacks, & May, 1999; Clapp & Gazzaley, 2012; Gazzaley, Clapp, Kelley, McEvoy & Knight & D'Espsoto, 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005) and that distracting information needs longer to be processed in older than younger participants (Cashdollar, Fukuda, Bocklage, Aurtenetxe, Vogel & Gazzaley, 2013; Clapp & Gazzaley, 2012;Clapp & Gazzaley, 2012; Clapp, Rubens, & Gazzaley, 2010; Fukuda & Vogel, 2009; Gazzaley et al., 2005; Minamoto, Osaka & Osaka, 2010). Interestingly, the impact of external distractions differentially affects performance on tasks with internal, as opposed to external, attentional orientations, with older participants selectively impaired in a mental rotation task during which external auditory irrelevant information was presented (Ziegler, Janowich, & Gazzaley, 2018). Although in the present study the visual stimulus on the screen is task relevant and participants should focus their attention on it, it might create an attentional anchor which older participants might find more difficult to disengage attention from. It is therefore possible that the systematic delay observed in older participants in the present study is not only driven by the increased time needed to create an internal representation of the stimulus but also by their ability

to disengage attention from the external stimulus and direct it on its internal representation for the mental rotation process.

In sum, the present ERP study investigated the time course of MR during a letter rotation tasks in younger and older adults. The present findings demonstrated that one source of the age-related slowing observed in previous behavioural MR tasks is linked to the initial phase of MR. Specifically, delayed RRN components were observed for both the normal and mirror letter conditions in the older as compared to younger participants. This finding shows that older participants need longer to start the processes of MR possibly because of a prolonged phase of stimulus encoding and/or selective difficulties in directing attention away from the external stimulus and towards its internal mental representation.

Chapter 5

Normal-mirror difference in Mental Rotation

5.1 Experiment 8 Introduction

In all the three ERP studies reported above (Experiment 2, 3 and 7), differential performances were detected in normal and mirror trials, which raised our interest to dig out whether different neural mechanisms underlying MR processing with normal and mirror objects. This research question has raised some interest recently suggesting that distinctive neural mechanisms underlie these two processes of MR (Hamm et al., 2009; Martinaud et al., 2016). However, to the best of our knowledge, the mechanisms of these two MR processes are still uncovered. For example, an additional "flip-over" process has been suggested to occur in mirror rotation, at a different time for different rotation angles (Hamm et al., 2009; Quan et al., 2017). Yet, no study has proved this hypothesis. Therefore, the present experiment was aimed at exploring specifically the time course of this additional process in MR of mirror stimuli for different rotation angles. Exploring the normal-mirror difference in MR processing, ageing and VVI,

was not an aim of the present experiment. This interesting question could be explored in future studies.

Recently, researchers have started to focus on the differences in MR processes observed during normal and mirror letter rotation. Typically, in behavioural MR studies, RTs are longer on mirror than normal stimuli trials (e.g. Cooper & Shepard, 1973; Kung & Hamm, 2010). The mirror-normal difference is also reported in ERP studies (Hamm, Johnson & Corballis, 2004; Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017). Hamm and colleagues (2004) first reported that the onset of RRN was delayed in the mirror compared to the normal condition. Similarly, Núñez-Peña and Aznar-Casanova (2009) found the modulation of RRN amplitudes measured between 400-500ms by rotation angle was more evident during normal than mirror letter rotation.

To interpret the longer RTs observed on mirror trials, Cooper and Shepard (1973) proposed that participants tend to prepare a 'normal letter' response by default at the beginning of a trial. Therefore, on mirror trials, this response has to be suppressed before the correct response can be executed. Thus longer RTs on mirror as compared to normal trials are caused by this extended response selection/execution process. However, to explain the normal-mirror behavioural difference other researchers have postulated the presence of an additional cognitive sub-process during the mental rotation of mirror as compared to normal letters (Alivisatos & Petrides, 1997; Corballs & McMaster, 1996). More specifically, mirror letters are also rotated

out of the plane after the rotation in the plane (planar rotation), so that they can be fully normalized (Corballis & McMaster, 1996; Quan et al., 2017). This process labelled 'flip-over' therefore prolongs RTs.

The "flip-over" hypothesis has been recently used to interpret the ERP differences observed between normal and mirror letter rotation. When ERPs elicited by upright normal letter were subtracted from those elicited by mirror letters, a negative-going waveform occurring between 400 and 500ms post-stimulus was observed. Because this component has a similar polarity and scalp distribution as the RRN which considered a marker of planar rotation, this negative ERP component was suggested to reflect the additional flip-over process occurring during mirror letter rotation (Hamm et al., 2004; Núñez-Peña and Aznar-Casanova, 2009). Accordingly, the fact that the RRN was delayed and/or less modulated by rotation angle on mirror than normal trials was interpreted as evidence for the additional non-planar rotation. Thus, while participants perform both a planar and a non-planar rotation on mirror trials, they only complete a planar rotation on normal trials. It was therefore suggested that the RRN in the mirror condition was at least in part cancelled out by the correlates of the out-of-plane 'flip-over' rotation which are elicited in the upright mirror condition when this is used as a baseline for the RRN calculation (Hamm et al., 2004; Núñez-Peña and Aznar-Casanova, 2009). This interpretation is based on the assumption that the planar rotation indexed by the RRN begins at the same time for

normal and mirror letters and that this process overlaps temporally with the non-planar rotation on mirror trials.

Although this hypothesis has been used to explain the delay in MR onset observed in mirror as compared to normal trials (Hamm et al., 2004; Núñez-Peña and Aznar-Casanova, 2009), it is not fully supported by evidence. ERP studies have shown that the difference between mirror and normal trials (reflecting the non-planar rotation) starts later with increasing rotation angles. This observation has led researchers to suggest that the out-of-plane (non-planar) rotation occurs after the planar rotation (Núñez-Peña and Aznar-Casanova, 2009; Quan et al., 2017), allowing participants to fully normalise mirror letters after the planar rotation. Moreover, such normal-mirror difference was absent for larger rotation angles (Núñez-Peña and Aznar-Casanova, 2009; Quan et al., 2017). It has been further suggested this is because the non-planar rotation occurs sequentially after the planar rotation for smaller angles but in parallel for larger angles. However, to our best knowledge, this temporal relationship between planar and non-planar rotation has not been tested.

Therefore, the current experiment employs the standard letter rotation paradigm as used in Núñez-Peña and Aznar-Casanova (2009). The primary aim is to investigate the temporal relationship between planar and non-planar rotation during the MR process of mirror letters, an important issue associated with the fundamental question of how normal-mirror judgments are made in MR tasks. Gleaned from the existing literature, we hypothesized that the non-planar rotation of mirror letters occurs

at different time relative to their planar rotation for letters presented at different angles. More specifically, we investigate whether, as suggested in the previous literature (Núñez-Peña and Aznar-Casanova, 2009; Quan et al., 2017), that the non-planar rotation occurs sequentially after the planar rotation for smaller rotation angles, whereas for larger angles these two processes occur in parallel.

5.2 Method

5.2.1 Participants

Forty-one paid participants were recruited from the University of Edinburgh. Ten participants had to be excluded because less than 50% trials remained after artefact rejection. Thus 31 participants (15 women), between 18 and 28 years of age (mean $= 22.3 \pm 0.9$ years old) remained in the sample for data analyses. All participants were right-handed and had normal or corrected-to-normal vision. Informed consent was obtained.

5.2.2 Stimuli and Experimental procedure

Stimuli and procedure was identical in Experiment 2 and 7 (see Figure 2-6).

5.2.3 EEG Recording and Pre-processing

EEG recording and pre-processing was identical in Experiment 2 and 7 as well.

5.2.4 Data Analysis

Two 2 × 6 repeated-measures analyses of variance (ANOVA) were performed on accuracy rates and correct response times averages (RTs) using rotation angle (0°, 30°, 60°, 90°, 120°, 150°)[14] and stimulus type (normal or mirror) as within-subjects factors. The Greenhouse- Geisser correction for sphericity violation was applied when appropriate. Simple effect tests were performed in the presence of a significant interaction. Orthogonal polynomial contrasts were conducted to discover the linear or quadratic trend of variables. If RTs were linearly corrected with rotation angles, MR rates were estimated as the slope of the regression line for RTs of rotation angles and compared between each stimulus types.

The first step of ERPs analysis process was similar to that described in Núñez-Peña and Aznar-Casanova's experiment (2009). ERPs mean amplitudes were computed for successive 50ms-interval separately for each rotation angle and each stimulus type from 300 to 1000ms post-stimuli collapsed across ten electrodes (CP1/2, CP3/4, P1/2, P3/4, CPz, Pz). Laterality was not taken into account as the normal-mirror difference was consistently emerged larger at central (Pz, CPz) than left (CP3, P3) of right sites (CP4, P4) in the initial analysis[15].

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14 Initial analysis of behavioural and EEG data was performed to test symmetry. However, no asymmetries main effect or interactions detects. Therefore, data were collapsed into six rotation angles (0°, 30°, 60°, 90°, 120°, 150°).

15 In the preliminary data analyses, laterality was taken into account with left-, central- and right-central-parietal sits (pooled over CP3 and P3, CPz and Pz, and CP4 and P4 respectively). Main effects of laterality emerged to be significant in all the 50ms-intervals time windows measured between 300 and 1000ms, all Fs $\geq$ 3.96, ps $\leq$ .024, $\eta 2 \geq .12$, with larger ERP amplitudes at central as compared to left or right sites. However, there was no interaction relating to laterality found in any time window, all p-values $>$ .05.

To investigate the temporal relationship between planar and non-planar rotation for each rotation angle, separate ANOVAs were conducted for each rotation angle and for successive 50ms-intervals from 300 to 1000ms post-stimulus. Separate 2×2 repeated-measures ANOVAs with stimulus type (normal or mirror) and rotation angles (0° vs. rotated angle (X^{o})) as within-subjects factors were performed on the ERPs mean amplitudes computed separately for each rotation angle (30°, 60°, 90°, 120°, 150°) at central-parietal sites (CP1/2, CP3/4, P1/2, P3/4, CPz, Pz). In these analyses, main effects of rotation angle (significant difference between ERPs measured for 0° and X° rotation angles) reflecting the presence of planar rotation (enhanced negativity for rotated than upright letters) indexed the presence of the RRN component. The main effect of stimulus type (significant difference between normal and mirror letters) reflected the presence of non-planar rotation processes. We were specifically interested in the relative timing of planar and non-planar rotation processes and in possible interactions between these rotation processes. Following significant interactions between stimulus type (non-planar rotation) and rotation angle (planar rotation), post-hoc comparisons were carried out to explore the presence of rotation angle main effects (planar rotation) for each stimulus type as well as the main effects of stimulus type (non-planar rotation) for each rotation angle to explore the time course of these sub-processes for each angle. Bonferroni corrections were applied whenever appropriate. Greenhouse-Geisser corrections were used in case of sphericity violations.

Partial η^2-values for each significant main effects or interactions were reported as well as the corrected *p*-values.

5.3 Results

5.3.1 Behavioural Results

5.3.1.1 Accuracy rate

A significant lower accuracy rate emerged in normal letters (M = 93.7%, SE = 0.8) than in mirror ones (M = 95.1%, SE = 0.7), F (1, 30) = 4.76, p = .037, η^2 = .14. As clearly shown in the left panel of Figure 5-1, left panel, a main effect of rotation angle emerged, F (1.6, 46.9) = 32.96, p < .001, η^2 = .52, revealing the fact that the accuracy rate linearly decreased with increasing rotation angle, F (1, 30) = 40.26, p < .001, η^2 = .57. Furthermore, stimulus type was found to interact with rotation angle, F (1.9, 57.1) = 13.5, p < .001, η^2 = .31. Rotation angle main effect was more evident in the normal (F (1.6, 47.6) = 31.72, p < .001, η^2 = .51) and mirror condition (F (1.9, 56.4) = 7.27, p = .002, η^2 = 20).

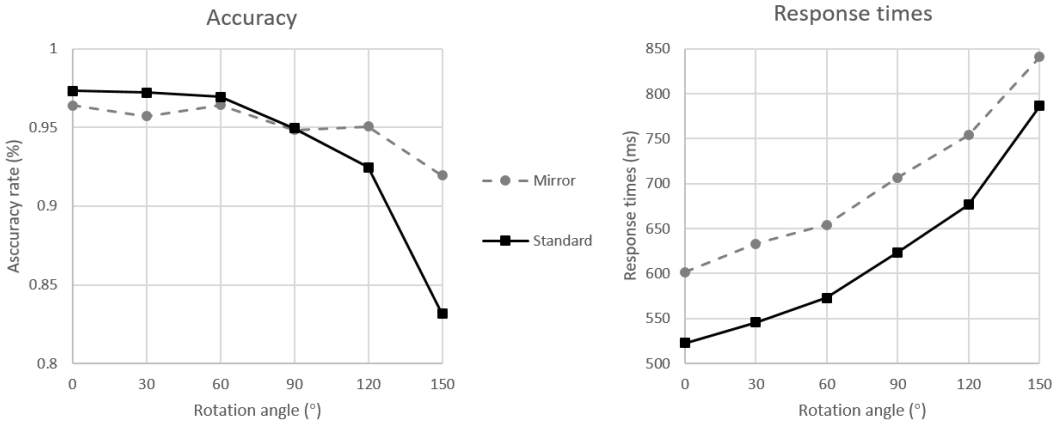

Figure 5-1. Behavioural performance in the normal (black solid line) and mirror conditions (grey dotted line). The left panel depicts the accuracy rate and the right panel shows the response times across all the rotation angles (0°, 30°, 60°, 90°, 120° and 150°) under two different experimental conditions.

5.3.1.2 Response times

Consistent with the existing literature, significantly longer RTs were observed in processing mirror (M = 698.29ms, SE = 21.17) than normal letters (M = 621.43ms, SE = 17.36), F (1, 30) = 63.53, $p < .001$, $\eta^2 = .68$. As shown in the right panel of Figure 5-1, a main effect of rotation angle also emerged on RTs, F (1.7, 49.6) = 209.7, $p < .001$, $\eta^2 = .88$. RTs increased with increasing rotation angles and were fit for a linear, F (1, 30) = 291.74, $p < .001$, $\eta^2 = .91$, and a quadratic trends, F (1, 30) = 63.07, $p < .001$, $\eta^2 = .68$.

In addition, the interaction of rotation angle and stimuli type emerged to be significant in the RTs analysis, F (2.7, 80.8) = 2.88, $p = .046$ $\eta^2 = .09$. The effects of rotation angle were reliably present in both the normal and mirror conditions, both Fs ≥ 113.52, ps < .001, $\eta^2 \geq .79$. In both conditions, the RTs functions departed from linearity (both Fs ≥184.69, ps < .001, $\eta^2 \geq .86$) and contained a quadratic component (both Fs ≥ 23.12, ps < .001, $\eta^2 \geq .44$). The subsequent slope analyses on RTs yielded significantly faster MR rates in the mirror (M = 1.44ms/degree, SE = .10) as compared to normal letter rotation (M = 1.66ms/degree, SE = .09), F (1, 30) = 10.361, p = .003, $\eta^2 = .026$. In addition, a larger intercept was observed for

mirror (M = 589.77ms, SE = 23.21) than for normal letters (M = 497.92ms, SE = 15.52), F (1, 30) = 48.25, $p < .001$, $\eta^2 = .62$.

5.3.2 Electrophysiological Results

Our primary interest in this experiment is the timing of planar and non-planar rotation and their possible interactions for each angle. Figure 5-2 shows the mean ERPs amplitudes pooled over centro-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for upright (0°) and rotated letters (X°) in the normal and mirror conditions respectively for each rotated angles (30°, 60°, 90°, 120° and 150°). In this figure, significant interactions between rotation angle and stimulus type are marked with red dotted line. The post-hoc comparisons (the effect of planar rotation in normal and mirror trials as well as the effect of non-planar rotation) following these interactions were depicted in Figure 5-3, Figure 5-4 and Figure 5-5 respectively.

Figure 5-3 and Figure 5-4 show the topographic mapping of the corresponding ERP difference between upright and rotated letters (*planar rotation*) separately for each rotation angle (30°, 60°, 90°, 120° and 150°) and for normal (Figure 5-3) and mirror letters (Figure 5-4) in successive 50ms time windows from 300 to 1000ms post-stimulus. The mean ERP amplitudes elicited at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for rotated (X°; dashed lines) and upright trials (0°; solid lines) are presented in the left panel separately for each rotated angle (30°, 60°, 90°, 120° and 150°).

Figure 5-5, right panel, shows the topographic mapping of the corresponding ERP difference between normal and mirror letters (*non-planar rotation*) presented separately for each angle (0°, 30°, 60°, 90°, 120° and 150°) in successive 50ms time windows from 300 to 1000ms post-stimulus. The left panel presents the mean ERP amplitudes collapsed across the trials at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for normal (solid lines) and mirror trials (dashed lines) separately for each rotation angle (0°, 30°, 60°, 90°, 120° and 150°).

As shown in Figure 5-3 and 5-4, the effect of *planar rotation* emerged later in mirror as compared to normal trials for letters rotated with 90° or 120°. However, such temporally delayed *planar rotation* in mirror as relative to normal trials is negligible for 150°. Moreover, different patterns were observed for smaller angles (30° & 60°): *planar rotation* was presence for the mirror, whereas no *planar rotation* is required for normal letters with small angles. In addition, as depicted in Figure 5-5, the *non-planar rotation* was observed to delay across angles as previously reported.

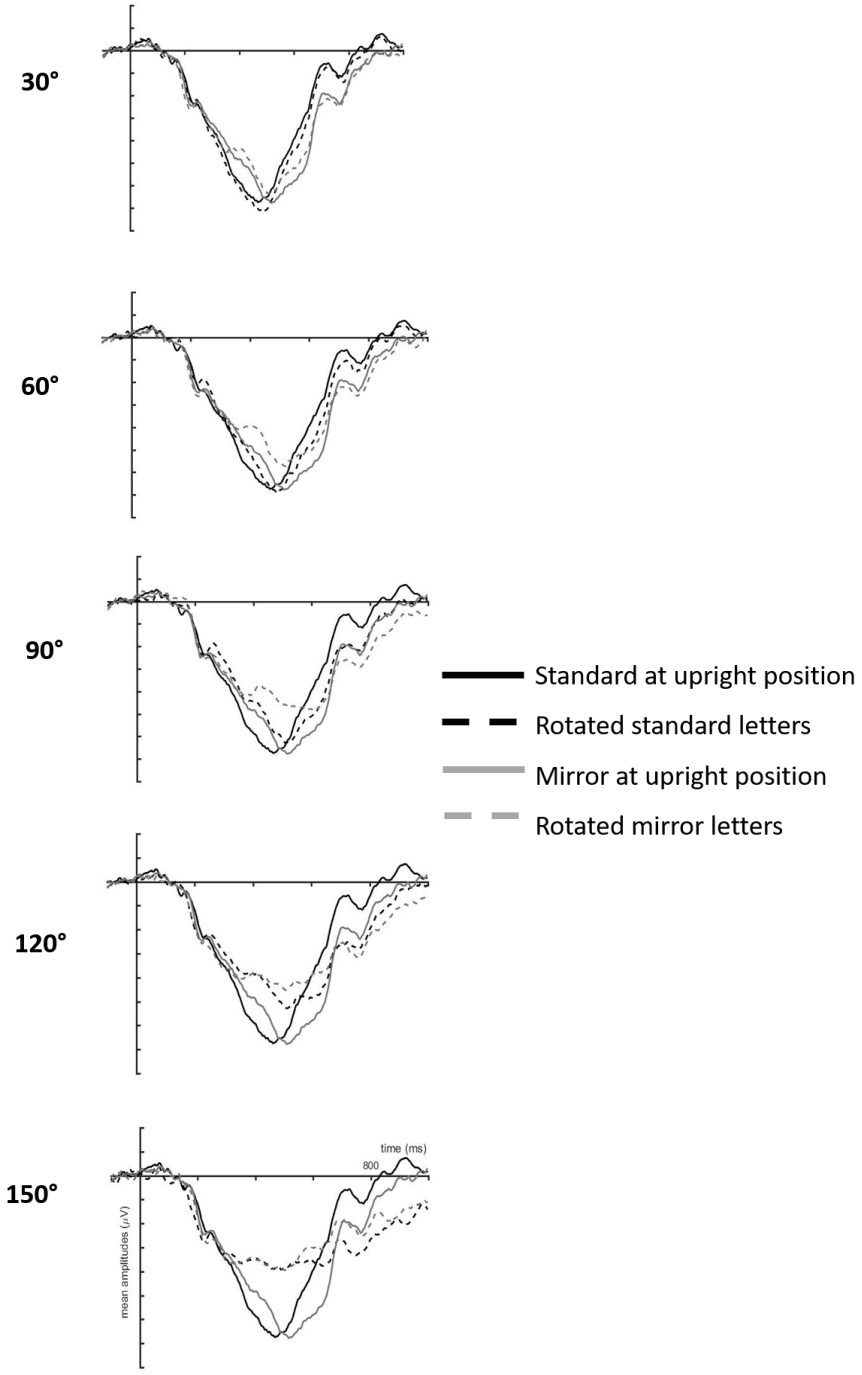

Figure 5-2. ERP mean amplitudes at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) shown separately for rotated (30°, 60°, 90°, 120°, and 150° rotation angles in different figures, dotted line) and upright letters (0°, solid line) and for normal (black) and mirror letters (grey).

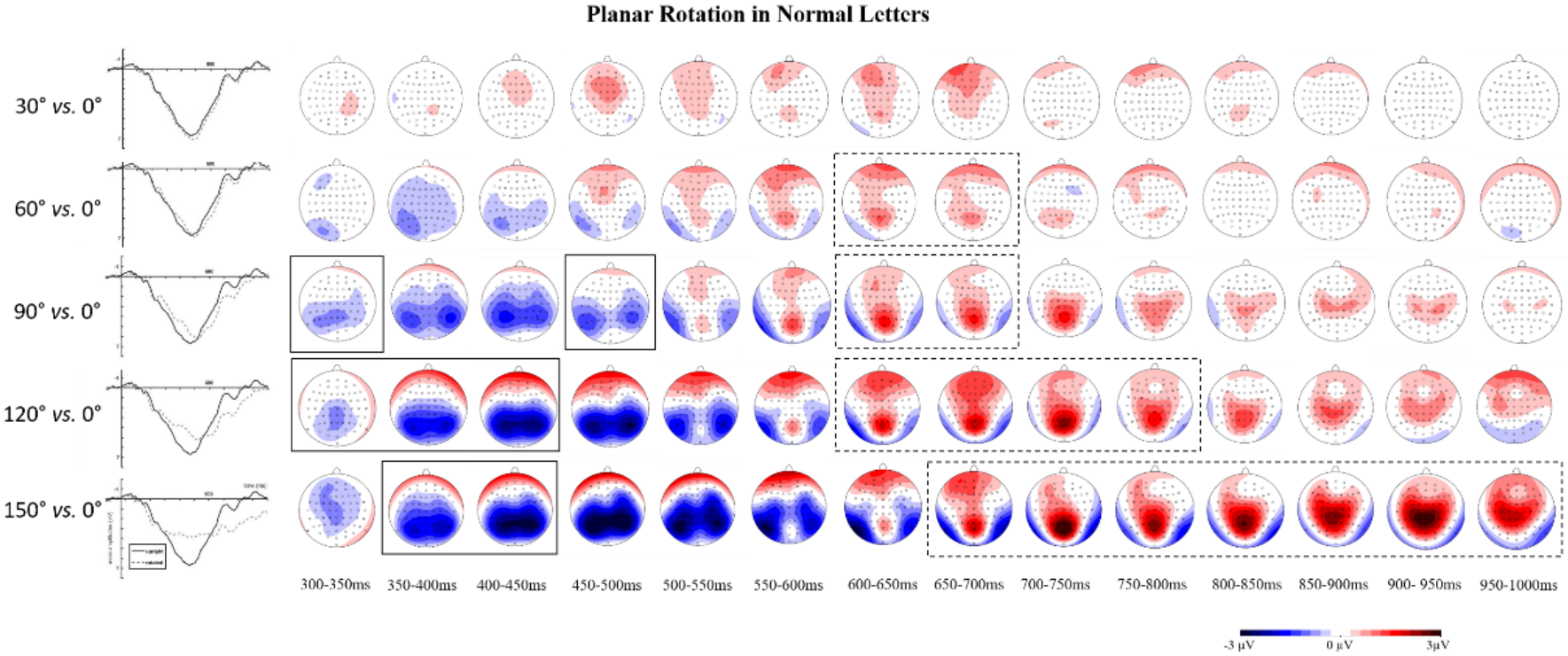

Figure 5-3. Brain potential performances in normal letter rotation. The left panel shows the mean ERP amplitudes elicited at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) by rotated (X°; dotted line) and upright letters (0°; solid line) in normal letters separately for each rotated angle (30°, 60°, 90°, 120°, and 150°). The right panel presents the topographic mapping of the corresponding ERP difference between upright and rotated letters (*planar rotation*) for normal letters in successive 50ms time windows from 300 to 1000ms post-stimulus separately for each rotated angle (30°, 60°, 90°, 120° and 150°). Intervals with significant effects of rotation angle within the intervals of rotation angle × stimulus type interactions for each angle were marked with black solid (more negative ERP amplitudes in rotated than upright letters) or dotted frame (more positive ERP amplitudes in rotated than upright letters).

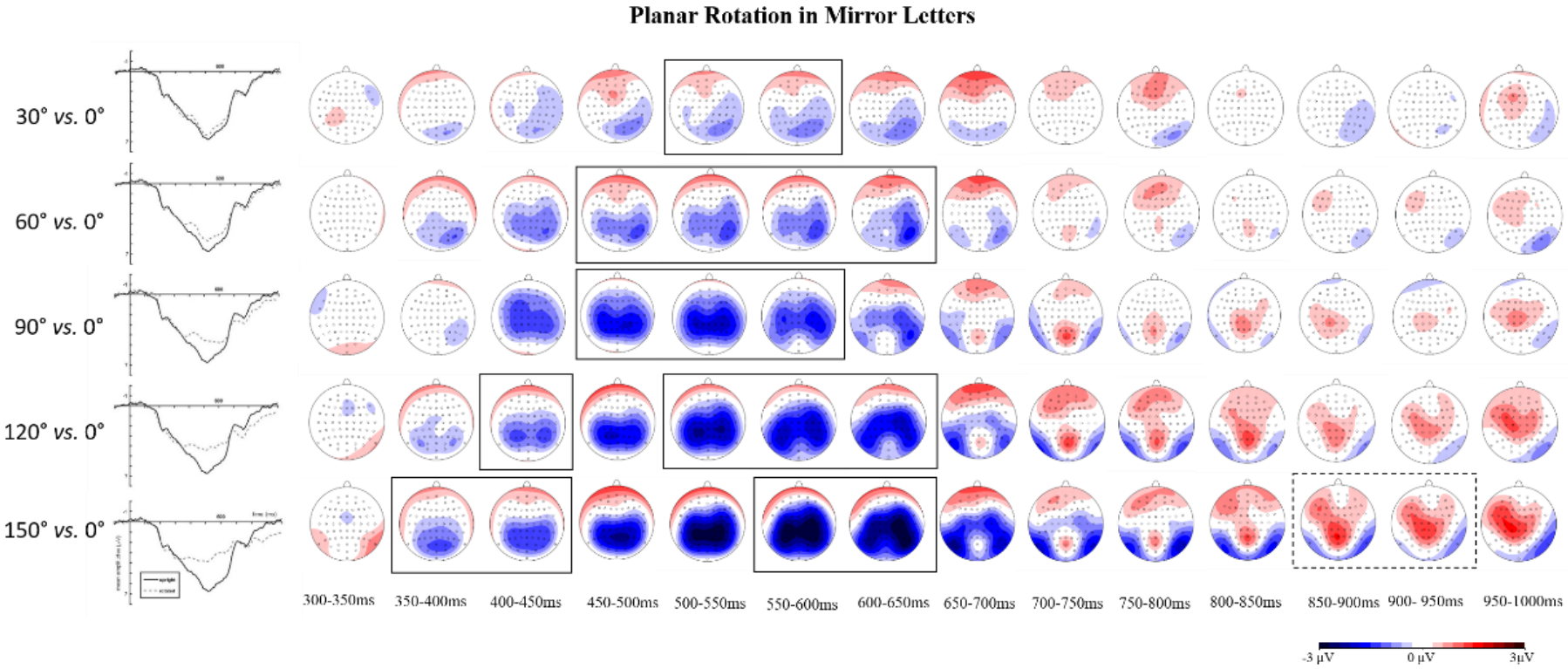

Figure 5-4. Brain potential performances in mirror letter rotation. The left panel shows the mean ERP amplitudes elicited at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) by rotated (X°; dotted line) and upright letters (0°; solid line) in mirror letters separately for each rotated angle (30°, 60°, 90°, 120°, and 150°). The right panel presents the topographic mapping of the corresponding ERP difference between upright and rotated letters (*planar rotation*) for mirror letters in successive 50ms time windows from 300 to 1000ms post-stimulus separately for each rotated angle (30°, 60°, 90°, 120° and 150°). Intervals with significant effects of rotation angle within the intervals of rotation angle × stimulus type interactions for each angle were marked with black solid (more negative ERP amplitudes in rotated than upright letters) or dotted frame (more positive ERP amplitudes in rotated than upright letters).

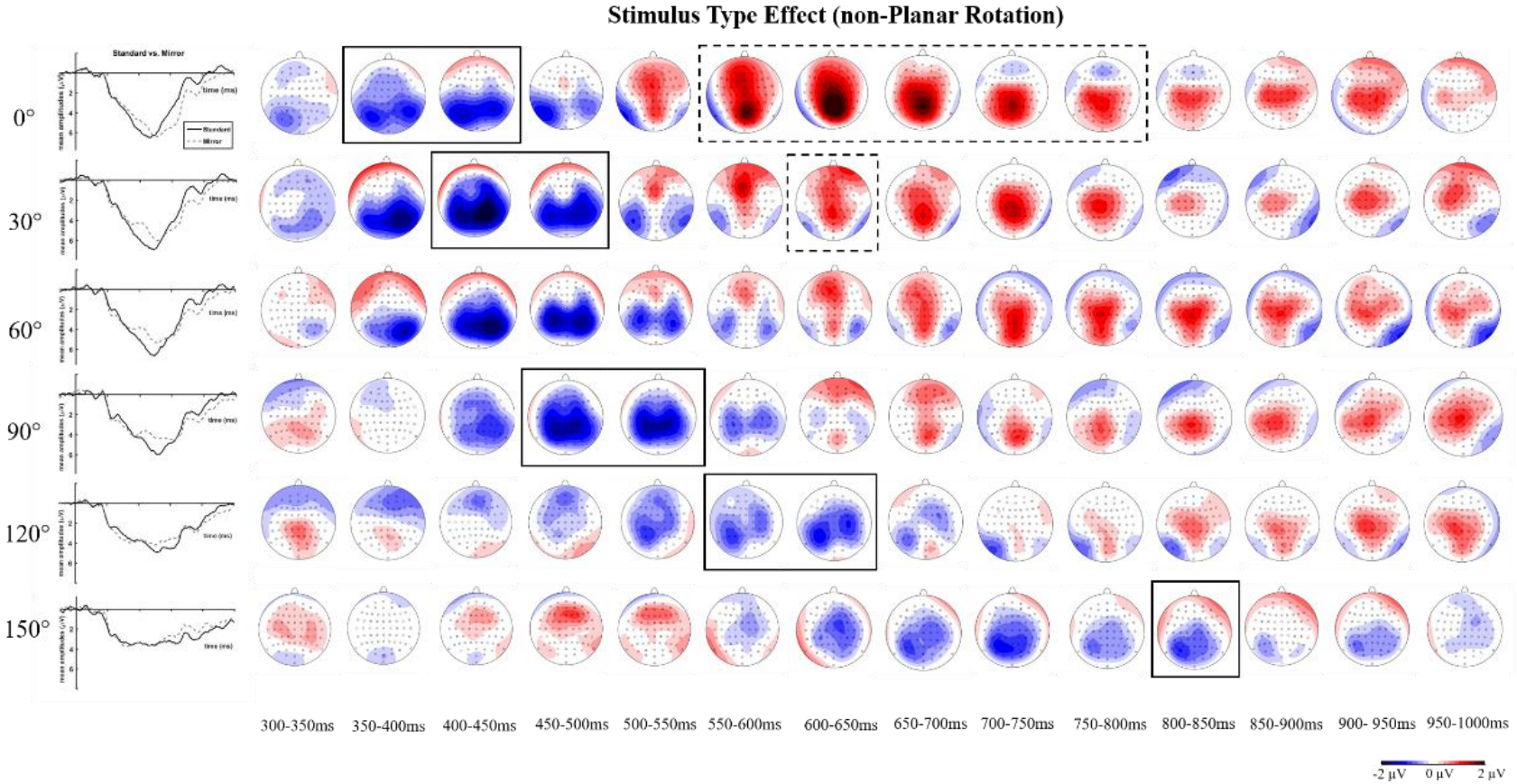

Figure 5-5. Brain potential performances for normal-mirror difference. The left panel shows the mean ERP amplitudes elicited at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) by mirror (dotted line) and normal letters (solid line) separately for each rotation angle (0°, 30°, 60°, 90°, 120°, and 150°). The right panel presents the topographic mapping of the corresponding ERP difference between mirror and normal letters (*non-planar rotation*) in successive 50ms time windows from 300 to 1000ms post-stimulus separately for each rotation angle (0°, 30°, 60°, 90°, 120° and 150°). Intervals with significant effects of stimulus type within the intervals of rotation angle × stimulus type interactions for each angle were marked with black solid (more negative ERP amplitudes in mirror than normal letters) or dotted frame (more positive ERP amplitudes in mirror than normal letters).

The statistical analysis performed on successive 50ms-interval from 300 to 1000ms post-stimulus supports all these observations. A summary of main effects of rotation angle, stimulus type or the rotation angle × stimulus type interactions as well as all the significant follow-up comparisons is presented separately for each rotated angle in Table 5.1 (30°), 5.2 (60°), 5.3 (90°), 5.4 (120°), and 5.5 (150°).

As summarised in Table 5.1, for letters rotated with 30°, main effect of rotation angle was present in the early time window measured between 300 and 350ms post-stimulus. ERP amplitudes were more negative for rotated (30°) than upright letters in this interval. In addition, main effects of stimulus type were obtained between 300 and 500ms with more negative ERPs amplitudes observed for mirror than normal letters. In addition, main effects of stimulus type were also present between 550 and 950ms post-stimulus. In this later interval, this main effect reflected the fact that ERP amplitudes were more positive for mirror than normal letters.

As depicted in Figure 5-2 and summarized in Table 5.1, rotation angle interacted with stimulus type in the time windows between 400 and 600ms. As revealed by the post-hoc analyses, rotation angle effects were observed for mirror (500-600ms) but not for normal letters (see Figure 5-3 and 5-4). In mirror condition, ERP amplitudes were more negative for rotated (30°) than upright letters. As presented in Figure 5-5, the effects of stimulus type observed between 400 and 500ms in rotated letters (30°) reflected the fact that ERP amplitudes were more negative for mirror than normal letters.

---- insert Table 5.1 about here----

As summarized in Table 5.2, main effects of rotation angle (350-500ms) and stimulus type (300-500ms and 550-950ms) were present for letters rotated with 60°. Compared to the main effects of rotation angle (more negative ERP amplitudes for rotated than upright letters) which occurred between 350 and 500ms post-stimulus, the stimulus type main effects emerged earlier (300-500ms) with more negative ERPs amplitudes observed in mirror than normal trials. By contrast, ERP amplitudes in the later interval (550-950ms) were more positive for mirror than normal letters.

In addition, the interactions of stimulus type and rotation angle were obtained between 450 and 700ms. As depicted in Figure 5-3, ERP elicited by normal letters were significantly positive for rotated than upright letters (600-700ms). By contrast, the ERP elicited by mirror letters were observed more negative for rotated (60°) than upright letters (450-650ms) (see Figure 5-4). As summarized in Table 5.2 and depicted in Figure 5-5, there was no effect of stimulus type emerged for rotated letters (60°).

----- insert Table 5.2 about here -------

For letters rotated with 90°, as summarized in Table 5.3, the rotation angle main effects were obtained in two intervals (300-550ms and 650-1000ms). In the earlier interval (300-550ms), ERP amplitudes were more negative for rotated (90°) than upright letters. The opposite pattern was observed in the later phase (650-1000ms) with more positive ERP amplitudes observed for rotated (90°) than upright letters. The main effects of stimulus type were obtained between 350 and 500ms and between 600 and 950ms. ERP amplitudes were more negative for mirror than normal letters in the earlier interval (350-500ms), whereas in the later interval (600-950ms) more positive ERP amplitudes were observed for mirror than normal letters.

As depicted in Figure 5-2, the stimulus type interacted with rotation angle between 300 and 350ms and between 450 and 700ms. ERP elicited by normal letters were observed more negative for rotated (90°) than mirror letters between 450 and 500ms. By contrast, in the later interval (600-700ms), the presence of the rotation angle effect for normal letter reflected the fact that ERP amplitudes were more positive for rotated (90°) than normal letters. In addition, ERP elicited by mirror letters were observed more negative for rotated (90°) than normal letters between 450 and 600ms. The stimulus type effects were also obtained for rotated (90°) letters between 450 and 550ms with more negative ERP amplitudes observed for mirror than normal letters.

-------insert Table 5.3 about here-------

For letters rotated with 120°, as summarized in Table 5.4, the rotation angle main effects were present between 350 and 600ms and between 650 and 1000ms. In the earlier interval (350-600ms), ERP amplitudes were more negative for rotated (120°) than upright letters. By contrast, ERP amplitudes were observed more positive for rotated (120°) than upright letters in the later interval (650-1000ms). In addition, the main effects of stimulus type were observed between 400 and 500ms with more negative ERP amplitudes observed for mirror than normal letters. By contrast, this stimulus type main effect in the later interval (550-950ms) reflected the fact that ERP amplitudes were more positive for mirror than normal letters.

As summarized in Table 5.4, the interactions of stimulus type and rotation angle emerged in two time windows (300-450ms and 500-800ms). For normal letters, as depicted in Figure 5-3, the effects of rotation angle were present between 300 and 450ms and between 600 and 800ms. ERP amplitudes were observed more negative for rotated (120°) than upright letters in the earlier interval (300-450ms). The opposite pattern was obtained in the later interval (600-800ms) with more positive ERP amplitudes for rotated (120°) than upright letters. The effects of rotation angle were also obtained for mirror letters between 400 and 450ms and between 500 and 650ms post-stimulus with more negative ERP amplitudes observed for rotated (120°) than upright letters. In addition, as depicted in Figure 5-5, the stimulus type effects were

present for rotated letters (120°) between 550 and 650ms. ERP elicited by mirror letters were observed more negative for mirror than normal letters in this interval.

-------insert Table 5.4 about here-----

For letters rotated at 150°, as summarized in Table 5.5, both rotation angles (350-650ms and 700-1000ms) and stimulus type main effects (350-450ms and 500-650ms) were obtained. As depicted in Figure 5-3, the rotation angle main effect in the earlier interval (350-650ms) reflected the fact that ERP amplitudes were more negative for rotated (150°) than upright letters. By contrast, ERP amplitudes showed the opposite pattern in the later interval (700-1000ms) with more positive ERP amplitudes for rotated (150°) than upright letters. In addition, the presence of stimulus type main effect between 350 and 450ms post-stimulus reflected the fact that ERP amplitudes were more negative for mirror than normal letters, whereas in the later interval (500-650ms) the opposite pattern was obtained with more positive ERP amplitudes for mirror than normal letters.

In addition, as summarized in Table 5.5, rotation angle interacted with stimulus type between 350 and 450ms and between 550 and 950ms post-stimulus. Rotation angle effects were obtained for both normal (350-450ms) and mirror trials (350-450ms and 550-650ms) with more negative ERP amplitudes observed for rotated (150°) than mirror letters. In the later phase, the effects of rotation angle were also present for both normal (650-950ms) and mirror trials (850-950ms). However, in these later intervals, more positive ERP amplitudes were observed for rotated (150°) than upright letters.

Moreover, as depicted in Figure 5-5, the stimulus type effects were present for rotated letters (150°) between 700 and 750ms and between 800 and 850ms with more negative ERP amplitudes observed for mirror than normal letters.

------insert Table 5.5 about here-----

5.4 Discussion

The present experiment addresses the normal-mirror difference in MR processing by comparing the timing of the planar rotation in normal and mirror trials and investigating the temporal relationship between planar and non-planar rotation in mirror trials for each rotation angle. To this end, the time courses of the planar rotation in normal, the planar and non-planar rotation in mirror trials were explored for each angle in 50ms interval from 300 to 1000ms post-stimulus.

We first replicated the largely documented normal-mirror difference in behavioural measures (e.g. Cooper & Shepard, 1973; Kung & Hamm, 2010) in the present experiment. Longer RTs were obtained in mirror than normal trials. Moreover, more errors were observed in normal as compared to mirror trials.

Our primary interest in the present experiment was to explore the temporal relationship of the three rotation processes: 1) planar rotation in normal letters; 2) planar rotation in mirror letters and 3) non-planar rotation in mirror letters. Therefore, we focused on the post-hoc comparisons of the stimulus type × rotation angle interactions for each rotation angle in successive 50ms interval from 300 to 1000ms

post stimulus where the time courses of these three rotation processes were investigated.

As revealed by the post-hoc comparisons between upright and rotated letters, more negative ERP amplitudes for rotated than upright letters were found in both normal (see Figure 5-3) and mirror letters (see Figure 5-4). This is consistent with the observation in previous ERP studies (Heil, Rauch, & Hennighausen, 1998; Heil & Rolk, 2002) indicating that planar rotation was required for both normal and mirror letters processing, though difference was also obtained.

As depicted in the black solid frame in Figure 5-3 and summarized in Table 5.1 and 5.2, rotation angle effects were present in almost all rotation angles for normal letters except for the smaller angles (30° and 60°). On the other hand, such rotation angle effects were obtained in all angles in mirror letters. The absence of the rotation angle main effect suggested that no MR processing is required for participants to make parity judgment for these small angle normal letters. This is consistent with the observation in RTs function which departs from linearity and contains a quadratic component as observed in the present experiment as well as in the existing literature (Hamm et al., 2004; Milivojevic, Hamm & Corballis, 2011) and provide ERPs finding supporting the idea that participants can - up to a certain degree - judge the parity of the familiar normal letters with smaller angles directly without mental rotation (Cooper & Shepard, 1973; Koriat & Norman, 1985). For 90° and 120°, as can be seen clearly in Figure 5-3 and 5-4 and summarized in Table 5.3 and 5.4, this rotation angle main

effect was observed to delay in mirror trials. This delayed rotation angle effect was consistent with the observations in previous ERP studies (Hamm et al., 2001; Heil & Rolk, 2002; Quan et al., 2017) suggesting that the planar rotation starts later in mirror as relative to normal letters. Interestingly, for letters rotated with 150°, as summarized in Table 5.5, the rotation angle effect emerged at the same time for normal and mirror letters (see Figure 5-3 and 5-4). This indicated that the planar rotation starts at the same time in processing normal and mirror letters rotated with 150°. All these results together revealed a different temporal relationship of planar rotation in normal and mirror condition for different angles as indicated by the post-hoc comparisons between upright and rotated letters.

In addition, as revealed by the post-hoc comparisons of ERP elicited by normal and mirror letters directly, negative-going waveforms were found for almost all angles except for 60° (see Figure 5-5). This negative-going ERP component has been reported in the previous literature and suggested correlated with the non-planar rotation in mirror letters (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009). Moreover, as can be seen clearly in Figure 5-5, this normal-mirror difference was observed starting later with increasing rotation angles. This is consistent with the observation in Núñez-Peña et al. (2009) and Quan et al.'s experiment (2017) suggesting that the non-planar rotation starts later with increasing rotation angles.

Different temporal relationship between the planar and non-planar rotation in mirror letters were found for different rotation angles when comparing the time course

of these two rotation processes in mirror condition separately for each angle. For smaller angles (30° and 60°), as depicted in Figure 5-4 and 5-5 and summarized in Table 5.1 and 5.2, the stimulus type effects emerged in earlier interval (400-500ms for 30°; 300-450ms for 60°) whereas the rotation angle main effects emerged in a later interval (500-600ms for 30°; 400-650ms for 60°) without any or at least with little temporal overlap. This result is inconsistent with the suggestion in previous studies (Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017) that to judge the parity of an object with smaller angles the non-planar rotation process ("flip-over") occurs first, followed by the planar rotation normalizing the rotated letters to the canonical position. For 90°, the effects of rotation angle and stimulus type emerged at the same time (in 450-500ms interval). This finding suggests that to process mirror letters rotated with 90°, the planar and non-planar rotation starts at the same time and these two processes occur in parallel. For 120°, as can be seen clearly in Figure 5-4 and summarized in Table 5.4, the rotation angle effect started to emerge in earlier intervals between 400 and 450ms and between 500 and 650ms as relative to the stimulus type effects which emerged between 550 and 650ms. However, as noted, unlike the observation in smaller angles, the effects of rotation angle and the effects of stimulus type emerged at the same time in the later phase between 550 and 650ms post-stimulus. These findings suggest that for letters rotated with 120°, participants started to rotate the stimuli in plane first and at some angle process planar and non-planar rotation processes in parallel until the stimuli normalized to the canonical view. Similarly, for 150°, the

rotation angle effects started to present in an earlier interval (350-450ms and 550-650ms) as relative to the effects of stimulus type (700-750ms and 800-850ms) without any temporal relationship. These results suggest that in processing letters rotated with 150°, planar rotation occurs first followed by the non-planar rotation to fully normalize this rotated mirror letters.

All in all, these findings suggest that the non-planar rotation occurs at different time as relative to the planar rotation for different rotation angles. Planar rotation occurs sequentially after the non-planar rotation for smaller angles (30° and 60°); for 90°, planar and non-planar starts at the same time and occurs in parallel; for larger angles (120° and 150°), planar rotation occurs earlier than the non-planar rotation. Specifically, for 120°, planar and non-planar rotation are carried out in parallel in the later phase (550-650ms). For 150°, non-planar rotation start to process until the planar rotation process finished.

This picture is different from that suggested in the previous studies (Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017) in which the non-planar rotation was suggested to occur after the planar rotation for smaller angles and in parallel with the planar rotation for larger angles. By explicitly exploring the temporal relationship between planar and non-planar rotation in mirror letters for each angle, we uncovered a more complex cognitive process underlying MR for mirror letters.

Previously, the delayed onset of RRN observed in mirror as compared to normal letters were suggested due to the cancel out by the additional non-planar

rotation (Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017). Though we did not test the RRN onset in the present experiment, we replicated this observation by comparing the timing course of planar and non-planar rotation directly but only for larger angles. Moreover, such delayed RRN in mirror than normal letters could not be fully explained by the non-planar rotation which occurs at a relative later phase. Future studies could further explore the possible reason to account for the delayed RRN onset in mirror than normal letters. The neural correlate of the non-planar rotation could be verified as well in future studies.

The finding in the present experiment provided a big picture on MR process of mirror letters which are complexly driven by planar and non-planar rotation occurring temporally different for each rotation angle, facilitating our understanding on the neural mechanism underlying MR processing with normal and mirror objects. Based on this finding, we therefore, suggest future ERP studies to use the normal trials only when the MR process is investigated.

Chapter 6

General Discussion

This dissertation set out with the aim of testing the hypothesis that multiple strategies could be adopted in addressing the requirements of cognitive tasks, in particular of MR, to reconcile the long-lasting imagery debate. To this end, MR was used throughout this dissertation since it is a typical task for mental imagery. In Chapter 1, five relevant areas of study were reviewed: cognitive processes underlying MR processing; strategy selection in MR tasks; individual differences in strategy selection in MR; ageing effects in MR; and MR processing for identical and mirror images. These areas of study are fundamental to the points of interest investigated in Chapters 2, 3, 4 and 5 addressing individual differences and aging effects in MR. In addition, two more experiments were conducted to further explore the mechanisms underlying MR processing.

6.1 Individual differences in MR

We then examined the role of visual imagery in MR tasks by exploring the individual difference in MR tasks in the first three experiments presented in Chapter 2. Participants were grouped into higher and lower VVI individuals according to their subjective reports on their visual imagery vividness and were assessed with a series of MR tasks to test whether they performed differently on these tasks.

Experiment 1 used a behavioural MR paradigm to demonstrate in which context, and how, individuals performed differentially in MR tasks. The stimulus complexity was manipulated by changing the segment number so that participants in this experiment were assessed with two types of stimuli, integrated (Standard condition) and multi-part objects (non-Standard condition). First, the behavioural performances were directly compared between higher and lower VVI individuals under different task demands and this yielded a significant result: systemic difference was detected between higher and lower VVI individuals in dealing with non-Standard multi-part objects, whereas they performed similarly in rotating the Standard integrated objects.

In addition, the strategy selection in MR tasks were specified under different task demands by testing the stimulus complexity effect on the slope of RTs function of rotation angle in each imagery group. The stimulus complexity effect was present in both imagery groups: higher VVI individuals rotated the multi-parts objects significantly faster as compared to the integrated ones, whereas a significantly slower MR rate was observed in lower VVI individuals in processing multi-part as compared to the integrated objects. These results suggest that higher VVI individuals were more

flexible relative to higher VVI individuals in generating a simplified representation of the visual stimuli and maintained this for further mental manipulation; individuals with lower VVI, on the other hand, were more likely to adopt piecemeal transformation in processing those multi-part objects.

The systemic difference between higher and lower VVI individuals in MR tasks was further confirmed in the following ERP experiment. In Experiment 2, the time course of MR processing was directly compared between higher and lower VVI individuals to test the prediction that visual imagery ability is correlated with the pure MR process. An interesting result was yielded: a prolonged MR process was shown in lower VVI individuals, indicating that individuals with lower VVI required more time for MR processing before making a judgment as compared to those with higher VVI. This result supports the argument that visual imagery ability could modulate the MR performance.

Experiment 3 further provided direct evidence for the view that MR tasks could be completed in the absence of visual imagery (representation). From this point of view, the functional role of visual imagery could be better understood. M.X., a single case who subjectively reported loss of his visual imagery ability, was tested in a standard letter rotation task while EEG was recorded. If M.X. could successfully complete the MR tasks without depictive representations, the idea that visual imagery plays an essential role would be challenged. As expected, in the absence of visual or depictive representation, M.X. performed as well as his controls in processing both

normal and mirror letters. Surprisingly, rotation process was still required in M.X. in processing normal letters. It is possible that an alternative non-depictive format of mental representation was generated and such representation was employed in the pure MR process. On the other hand, M.X. did not adopt the typical MR processing in coping with mirror letters. Instead, he might, as described in Zeman et al.'s study (2010), have used an alternative cognitive strategy to successfully complete this MR task. The results in this single case experiment provided direct evidence for the long-lasting imagery debate, supporting the recent argument that visual imagery is not necessary in cognition, and multiple representations and strategies could be adopted in a cognitive task. Moreover, the results indicated two possibilities for completing MR tasks in the absence of visual imagery: either to maintain non-depictive representation (i.e. language-like or spatial information) while rotating or to use a totally different strategy (i.e. perceptually comparison) rather than MR processing.

To summarise, these experiments explored the role of visual imagery in MR, contributing to the ongoing imagery debate by carrying out one line of research (Experiment 1, Experiment 2 and Experiment 3). The findings in these three experiments revealed the correlate of visual imagery and MR processing. Specifically, as revealed in the behavioural study (Experiment 1), individuals with higher VVI are more flexible in generating the mental representation and therefore are more likely to simplify the task by generating a partial image in their minds and use this for further mental manipulation. Individuals with lower VVI, on the other hand, might find it

difficult to encode all the information presented by the visual stimuli and have to adopt piecemeal transformation to complete the MR tasks. This finding is consistent with what we observed in the ERPs studies (Experiment 2) in which a prolonged MR processing is observed in lower as compared to higher VVI individuals, suggesting that lower VVI individuals take longer in MR processing relative to higher VVI individuals. Moreover, the finding in Experiment 3 provided convincing evidence for the argument that visual imagery is not necessary in MR tasks by observing M.X. successfully complete the MR tasks (especially in mirror condition) without the presence of RRN, the neural correlate of MR processing. However, with a lack of the direct neural correlate of different strategies in MR tasks (i.e. piecemeal transformation or holistic strategy), it is impossible to indicate the strategy selection in ERPs studies based on the existing result to. However, this result provides a direction for exploration in future studies. For example, unfamiliar objects with different levels of complexity (integrated or multi-part) could be used in ERPs studies, as was done in Experiment 1, to explore the neural correlates of the different strategies used in MR tasks. Additionally, it is worth noting that the VVIQ2 was used to measure the visual imagery ability. As suggested in recent studies, this visual imagery questionnaire is primarily a measure of object rather than spatial imagery (Blajenkova et al., 2006; Blazhenkova et al., 2010); the separation of the higher and lower VVI individuals in these experiments reported in this thesis is mainly according to the object imagery which is a limitation of these experiments. To fully understand the functional role of visual

imagery in cognition, future work could be done to explore the functional role of spatial imagery in MR tasks.

6.2 Ageing effects in MR

Another main research question about how ageing affects MR was addressed in Chapter 4. Three empirical experiments presented in this chapter address this issue from two points of view: the ageing effect on the pure MR process and the non-rotation process.

In the light of the idea that multiple strategies could be adopted by different individuals, Experiments 5 & 6 focused on testing whether the widely documented ageing effect in MR could be accounted for in terms of different strategy selection. The stimulus complexity was manipulated, as suggested in Experiment 4, by changing the segment number in the arm-like cube stimuli (in Experiment 5) as well as in the polygons (in Experiment 6). According to the stimulus complexity hypothesis (Cooper, 1975), the effect of stimulus complexity was tested in each age group and yielded the following results: older adults showed a slower MR rate in these multi-part rather than integrated objects; the opposite results were obtained in the younger adults: they performed faster in multi-part as compared to integrated objects. In addition, similar performances were observed between younger and older participants in processing integrated objects. All these findings together provide evidence for the possibility that the strategy selection in MR may vary with age, especially in processing unfamiliar

and complex objects. It may be argued that older adults were more cautious compared to the younger ones. Therefore, they maintained all the information of the fragmented stimuli and slowed down the MR rate, whereas younger participants simplified the representation by encoding rotation-related information only in their minds' eyes. However, in this case, more errors would occur in larger rotation angles which is inconsistent with the findings in these experiments. Another factor, working memory, may explain this difference. The feature binding ability in working memory was found to decrease with age and this may possibly account for older adults, that they could not represent the whole image in their minds and therefore had to transform the image piece by piece. Future studies could be conducted to test this hypothesis.

Experiment 7 focused on the question of how aging affects the non-rotation process. In this experiment, we directly compared the time course of MR processing between younger and older adults. The onset of MR process was found to be delayed in older as compared to younger adults. This longer time for older adults in the initial phase before MR pure process is possibly because they require more time in stimulus encoding or have selective difficulties in directing attention away from the external stimulus and towards its internal mental representation. The finding demonstrated that the age-associated slowing observed in previous behavioural experiments is linked to the initial phase before the pure MR process.

In sum, the widely documented ageing effect in MR tasks was re-examined by exploring this effect on both rotation (Experiment 5 & 6) and non-rotation processes

(Experiment 7) and this provided a new standpoint from which to look again at this ageing effect. In the literature, an age-related slowing was consistently observed in the rotation processes as reflected by the slope measure. The findings from Experiments 5 and 6 focused on this pure MR process and provided an alternative account for this slowing in terms of the different strategy selection by younger and older adults. On the other hand, an age-associated slowing in MR was also reported in the literature in the non-rotation processes as indicated by a larger intercept observed on the estimates intercept measure in RTs function of rotation angle. Due to the complex cognitive process underlying MR tasks, such slowing could derive from the initial phase (i.e. stimulus perception and discrimination) or the later phase (i.e. parity judgment or response execution). The results from Experiment 7 indicated one source of this age-related slowing in the non-rotation process linking to the initial perceptual phase. The question of whether age affects the later phase (judgment making and executive function) which occurs after the pure MR process would also be interesting to explore in future studies to facilitate our understanding of the ageing effect in MR tasks.

6.3 Post-hoc explorations on mechanism of MR

6.3.1 The effect of visual stimuli on strategy selection in MR

Although some findings in the first three experiments supported the argument that different representations and strategies could be adopted by different individuals, whether and how the strategy selection in MR tasks varies with different types of visual

stimuli was still unclear. To address this issue, in Experiment 4, as described in Chapter 3, two properties of polygons were investigated to test which property was more predictable for strategy selection in MR tasks. The stimulus complexity was manipulated by changing either the vertices number or the segment number of the polygon. Main effect of segment number was reliably found on the estimated slope measure of RT function, a suggested indicator of strategy selection in MR. The more segments involved, the slower the MR rate was. This result indicates that piecemeal transformation is found to be more likely to be adopted in processing multi-part objects. However, no vertices number main effect emerged suggesting that a holistic strategy is more commonly used for integrated objects. All these results together provide supporting evidence for the argument that multiple representations and strategies could be adopted in a cognitive task, and indicates that the strategy selection varies with the type of stimuli. Moreover, the mismatched foil was introduced to test its functional role in MR tasks. The main effect of segment number was observed on the estimated slope of RTs in the with-foil but not in the without-foil condition. This result verifies the role of these distractors in MR tasks that could force participants to encode all information of the visual stimuli, as predicted in previous research (Cooper & Podgorny, 1976; Folk & Luce, 1987).

6.3.2 Normal-mirror difference in MR

Since relatively little scientific attention has been focused on the difference between normal and mirror object rotations, the final empirical experiment in Chapter

5 of the dissertation was dedicated to this topic. Gleaned from the existing literature, it was predicted that the non-planar rotation occurs at a different time relative to the planar rotation for different angles. The findings in Experiment 8 proved this prediction by exploring the temporal relationship between planar and non-planar rotation in mirror condition. Specifically, for smaller angles, the non-planar rotation occurred at a relatively early stage followed by the planar rotation. For 90°, the planar and non-planar rotation started at the same time and occurred in parallel. For larger angles, however, the planar rotation started earlier and the non-planar rotation occurred in a relatively later phase in parallel with the planar rotation process. The results in this experiment uncovered a complex cognitive process underlying the mirror rotation, facilitating our understanding on normal-mirror difference in MR processing, that the mirror rotation is complexly driven by the planar and non-planar rotation which occur at different time points for different angles. This is useful practically, from a methodology point of view, for future ERPs studies to use normal trials only when the pure MR process is the point of interest.

1) The various types of visual stimuli, the typical cube stimuli used in Metzler & Shepard, 1971, the polygon stimuli,
2) Limited sample, especially in experiment 1, 4, 5 & 6

6.4 Future directions

We are convinced that some of the findings, from the methodological view, may inform future studies. Specifically, we presented results showing that changing

the segment number rather than the number of properties of an object is more likely to produce piecemeal transformation, whereas a holistic strategy is more likely to be adopted in coping with integrated objects. This result could be used in future studies in stimulus design if the complexity effect is considered. That is to say, the stimulus complexity, based on our results, would be manipulated by changing the segment number rather than the vertices number. This could be used in future studies in exploring the functional role of spatial imagery in cognition task by investigating the individual difference in strategy selection in MR tasks under different task demands. Alternatively, the Standard and non-Standard stimuli could be used in future ERPs studies to further explore the neural index for the different strategies used in MR tasks. Secondly, the results in Experiment 8 uncovered a complex cognitive process underlying mirror rotation with the non-planar rotation occurring at different time as relative to planar rotation for different rotation angles. Based on this result, we suggest using the normal trials only to analyse the MR processing in future studies, as typically used in behavioural studies.

Apart from the above-mentioned suggestions, the studies conducted for this thesis produced several directions for future studies. First, in the last empirical experiment, the planar rotation was observed to start later in mirror as compared to normal condition in 120°. Moreover, the non-planar rotation was observed to occur at a later phase as suggested in the literature (Hamm et al., 2004). Therefore, the delayed planar rotation in mirror than normal letters could not be fully explained by the effect

of non-planar rotation as suggested in previous literature that ERP elicited by the planar rotation is cancelled off by ERP elicited by the non-planar rotation in mirror letters (Hamm et al., 2004). In a recent combined fMRI-eye tracking study, the normal-mirror difference was found to occur at a very initial stage in stimuli processing before the pure MR process with a smaller functional field of view during stimulus perception in mirror than normal trials (Paschke, Jordan, Wüstenberg, Baudewig & Müller, 2012). It is possible that the initial processing/encoding of mirror letters takes longer than that of normal letters. This prolonged initial processing phase before MR proper in mirror letters might delay the subsequent onset of the planar rotation sub-processes. Therefore, differences between normal and mirror condition as reflected by a later RRN onset and longer RTs could be accounted for – at least in part – by a delay in the onset of MR proper in the mirror as compared to the normal condition. Future studies could be done to test this speculation to clarify whether, and which, specific sub-process is prolonged in mirror as relative to normal trials. Besides, it would be interesting to isolate the additional non-planar rotation in mirror trials in a future experiment to verify the neural correlate of such non-planar rotation process.

Secondly, as mentioned in the discussion in Chapter 4 on ageing effect in MR tasks, working memory might play a role in MR processing. In this context, the deficit or decreased working memory ability might account for the ageing effect. It would be interesting to test and clarify this speculation in future studies. In addition, the role of working memory in MR is still unclear. To understand the mechanism of how working

memory works in MR will help us better understand why MR performance declines with age. Working memory (WM) (Baddeley, 2003), particularly visuospatial WM (Logie, 1995) is conceived as a multicomponent mental workspace: a *spatial* component support memory for spatial locations and an *object* component support memory for stimulus appearance. MR is assumed to, at least partly, share a common cognitive and neural process with WM (Albers et al., 2013; Atance & O'Neill, 2001; de Vito & Della Sala, 2011). Hyun and Luck (2007) used a dual-task approach and found MR task interference was observed in the object WM system but not the spatial WM, suggesting that object WM was served as the substrate for MR. However, the standard letter rotation paradigm was used in their study. As we already know that differential mechanisms underlie MR processing with familiar and unfamiliar objects, it would be interesting to test the role of spatial and object WM in the unfamiliar object rotation. In addition, as revealed in the last experiment, differential mechanisms were underlying MR processing in normal and mirror trials. We could explicitly explore whether spatial and object WM works in unfamiliar object rotation in normal and mirror trials respectively.

6.5 Final conclusions and limitations

This thesis explored the individual differences and aging effects in MR as well as some fundamental questions on the mechanism underlying such process.

First, differential MR performance was observed across individuals with different levels of VVI. The results in Experiment 1 addressed the different strategy selections in lower and higher VVI individuals, especially in processing MR tasks with more complex objects. A prolonged MR processing was further detected in the following experiment (Experiment 2) in higher as compared to lower VVI individuals in a letter rotation task. In Experiment 3, the single case, MX, who subjectively reported loss of his visual imagery was assessed with a letter rotation task as well as his age, gender, IQ-matched controls. He performed as well as his controls in both standard and mirror letters. However, the typical linear RTs of rotation angle and the RRN, the biomarker for MR processing was absent in MX in processing mirror letters, while he performed comparable with his controls in standard letters, suggesting that MR processing is not necessary in a MR task. In sum, the results in all these three experiments together suggest that VVI plays a role and could mediate the performance in MR tasks.

Secondly, this thesis addresses several lines of behavioural research on MR, providing unique evidence supporting the recent argument that multiple formats of representations and strategies could be adopted in the cognition task (Pearson & Kosslyn, 2015). This hypothesis was explored by considering whether strategy selection in MR varies with individual difference (in Experiment 1), ageing (Experiment 5 and Experiment 6) and different types of stimuli (Experiment 4). Piecemeal transformation is more likely to be adopted in multi-part objects than

integrated ones. By assessing the MR performance in these two types of stimuli, both ageing and the visual imagery ability were found could affect the strategy selection in MR tasks. As revealed in Experiments 1, 5 and 6, younger individuals with higher VVI rely more on partial image transformation and produce a faster MR rate, whereas those with lower VVI or older adults are more likely to use piecemeal transformation. Then the next question is why younger and older adults tend to choose different strategies in MR tasks, and could this be accounted by the visual imagery ability? In Experiments 5 and 6, the VVI ability is controlled in these two experiments so that the difference in visual imagery may not account for this ageing effect on strategy selection in MR.

Thirdly, the largely documented aging effects in MR was further explored in this thesis. An alternative account for the age-related slowing in MR was tested and verified that different strategies could be adopted by younger and older adults (Experiment 5 & 6). In the following experiment with letter rotation (Experiment 7), MR processing was found to start later in older as compared to younger adults, which demonstrates one source of age-related slowing observed in behavioural experiment is linked with the initial phase occur before the pure MR.

Last not but not least, the differential neural mechanisms underlying standard and mirror letter rotation processes were further explored (Experiment 8). The suggested additional “flip-over” process in mirror rotation was found occur at different time as relative to the planar rotation for different rotation angles.

It is worth noting that though the significance levels are reliable, the relatively small sample size is possible limitation of some experiments in this thesis (especially in Experiment 1, 4, 5 & 6). In addition, aging effects and individuals differences were main factors taken into accounts. Future studies could also be carried out based on the current findings to explore other potential factors (i.e., gender, spatial ability or working memory) that might affect the default mode of the internal representation/ strategies in MR tasks.

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Appendix A- VVIQ2

Vividness of Visual Imagery Questionnaire 2

Visual imagery refers to the ability to visualize, that is, the ability to form mental pictures, or to "see in the minds' eye". Marked individual differences have been found in the strength and clarity of reported visual imagery and these differences are of considerable psychological interest.

The aim of this test is to determine the vividness of your visual imagery. The items of the test will possibly bring certain images to your mind.

You are asked to rate the vividness of each image by reference to the 5-point scale given below: No image at all/ Vague and dim/ Moderately clear and vivid/ Reasonably clear and vivid/ Perfectly clear & vivid as if I was actually seeing it. Familiarize yourself with the different categories on the rating scale. Throughout the test, refer to the rating scale when judging the vividness of each item separately, independent of how you may have done other items.

Complete all item for images obtained with your eyes CLOSED.

In answering items 1 to 4, think of some relative or friend whom you frequently see and consider carefully the picture that comes your mind's eye.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
1. The exact contour of face, head, shoulders and body.					
2. Characteristic poses of head, attitudes of body etc.					

3. The precise carriage, length of step, etc. in walking.
4. The different colours worn in some familiar clothes.

In answering item 5 to 8, think of the items mentioned in the following questions and rate the vividness of your imagination.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
5. The sun is rising above the horizon into a hazy sky.					
6. The sky clears and surrounds the sun with blueness.					
7. Clouds. A storm blows up, with flashes of lighting.					
8. A rainbow appears.					

In answering items 9 to 12, think of the front of a shop which you often go to. Consider the picture that comes before your mind's eye.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
9. The overall appearance of the shop from the opposite side of the road.					
10. A window display including colours, shape and details of individual items for sale.					
11. You are near the entrance. The colour, shape and details of the door.					
12. You enter the shop and go to the counter. The counter assist serves you. Money changes hands.					

In answering items 13 to 16, think of a country scene which involves trees, mountains and a lake.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
13. The contours of the landscape.					
14. The colour and shape of the trees.					
15. The colour and shape of the lake.					
16. A strong wind blows on the trees and on the lake causing waves.					

In answering items 17 to 20, think of being driven in a fast-moving automobile by a relative or friend along a major highway. Consider the pictures that comes into your mind's eye.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
17. You observe the heavy traffic travelling at maximum speed around your car.					

The overall appearance of vehicles, their colours, sizes and shapes.

18. Your car accelerates to overtake the traffic directly in front of you. You see an urgent expression on the face of the driver and the people in the other vehicles as you pass.

19. A large truck is flashing its headlights directly behind. Your car quickly moves over to let the truck pass. The driver signals with a friendly wave.

20. You see a broken-down vehicle beside the road. Its lights are flashing. The driver is looking concerned and she is using a mobile phone.

In answering items 21 to 24, think of a beach by the ocean on a warm summer's day. Consider the picture that comes before you minds' eye.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
21. The overall appearance and colour of the water, surf, and sky.					
22. Bathers are swimming and splashing about in the water. Some are playing with a brightly coloured beach ball.					
23. An ocean liner crosses the horizon. It leaves a trail of smoke in the blue sky.					
24. A beautiful air balloon appears with four people aboard. The balloon drifts past you, almost directly overhead. The passengers wave and smile. You wave and smile back at them.					

In answering items 25 to 28, think of a railway station. Consider the picture that comes before you mind's eye.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
25. The overall appearance of the station viewed in front of the main entrance.					
26. You walk into the station. The colour, shape and details of the entrance hall.					
27. You approach the ticket office, go to a vacant counter and purchase your ticket.					
28. You walk to the platform and observe other passengers and the railway lines. A train arrives. You climb aboard.					

Finally, in answering items 29 to 32, think of a garden with lawns, bushes, flowers and shrubs. Consider the picture that comes before your mind's eye.

	No image at all	Vague and dim	Moderately clear and vivid	Reasonably clear and vivid	Perfectly clear & vivid as if I was actually seeing it
29. The overall appearance and design of the garden.					
30. The colour and shape of the bushes and shrubs.					
31. The colour and appearance of the flowers.					
32. Some birds fly down onto the lawn and start pecking for food.					

Appendix B Information for distractors

Canonical	Foil 1	Foil 2	Foil 3	Foil 4	Mean Manipulate Amplitude
	0.26	0.25	0.25	0.30	0.26
	0.21	0.20	0.32	0.36	0.27
	0.36	0.24	0.26	0.21	0.27
	0.25	0.30	0.32	0.26	0.28
	0.29	0.26	0.29	0.23	0.27
	0.23	0.28	0.27	0.22	0.25
	0.24	0.21	0.29	0.16	0.23
	0.26	0.24	0.22	0.33	0.26
	0.26	0.24	0.34	0.28	0.28
	0.34	0.37	0.24	0.30	0.31

Appendix C: List of publications

Published:

Zhao, B., & Della Sala, S. (2018). Different representations and strategies in mental rotation. *Quarterly Journal of Experimental Psychology*, *71*(7), 1574-1583.[16]

Under review, revision invited:

Zhao, B., Della Sala, S., & Gherri, E. (under review). Visual imagery vividness and mental rotation of characters: an event related potentials study. *Neuroscience Letters.*[17]

Zhao, B., Gherri, E., & Della Sala, S. (under review). Age effects in mental rotation are due to the use of a different strategy. *Aging, Neuropsychology and Cognition.*[18]

Zhao, B., Della Sala, S., & Gherri, E. (under review). Age-associated delay in mental rotation processing. *Psychology and Aging*.[19]

Zhao, B., Zhu, C., & Della Sala, S. (under review). Which properties of the visual stimuli predict strategy in mental rotation? *Quarterly Journal of Experimental Psychology*.[20]

In preparation:

Zhao, B., Gherri, E., Zeman, A., & Della Sala, S. (in preparation). Mental rotation in the absence of depictive representation: a case report.[21]

Zhao, B. Della Sala, S., & Gherri, E. (in preparation). Different time courses of mental rotation process for standard and mirror characters: a latency shift account.[22]

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[16] Includes Experiment 1.

[17] Includes Experiment 2.

[18] Includes Experiment 5 and 6.

[19] Includes Experiment 7.

[20] Includes Experiment 4.

[21] Includes Experiment 3.

[22] Includes Experiment 8.

Table 5.1

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 30° from 300 to 1000ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	***Angle*** main effect (0° vs. 30°) Planar Rotation	***Stimulus Type*** main effect (normal vs. mirror) Non-planar rotation	***Rotation Angle*** × ***Stimulus Type*** interaction	**Follow-up Comparisons**			
				Angle main effect (0° vs. 30°) Planar Rotation		Stimulus Type (normal vs. mirror) Non-planar rotation	
				Normal letter	Mirror Letter	0º	30º
300-350ms	F (1, 30) = 4.61, p = .040, η^2 = .13	F (1, 30) = 8.17, p = .008, η^2 = .21	F (1, 30) = .01, p = .922, η^2 =.001				
350-400ms	F (1, 30) = .05, p = .82, η^2 = .002	F (1, 30) = 18.14, p < .001, η^2 = .38	F (1, 30) = 1.61, p = .21, η^2 = .05			F_c (1, 30) = 4.42, p_c = .044, η^2 = .20 N > M	F_c (1, 30) = 12.03, p_c = .002, η^2 = .34 N > M
400-450ms	F (1, 30) = .51, p = .48, η^2 = .02	F (1, 30) = 27.67, p < .001, η^2 = .48	F (1, 30) = 6.04, p = .020, η^2 = .17	n.s.	n.s.	F_c (1, 30) =7.15, p_c = .012, η^2 = .26 N > M	F_c (1, 30) = 20.27, p_c < .001, η^2 = .48 N > M
450-500ms	F (1, 30) = .07, p = .80, η^2 = .002	F (1, 30) = 9.48, p = .004, η^2 = .24	F (1, 30) = 6.06, p = .020, η^2 = .17	n.s.	n.s.	n.s.	F_c (1, 30) = 9.72, p_c = .004, η^2 = .31 N > M
500-550ms	F (1, 30) = .04, p = .841, η^2 = .001	F (1, 30) = .51, p = .48, η^2 = .02	F (1, 30) = 12.72, p = .001, η^2 = .30	n.s.	F_c (1, 30) = 4.61, p_c = .040, η^2 = .20 0 > 30	n.s.	n.s.
550-600ms	F (1, 30) = .27, p = .610, η^2 = .01	F (1, 30) = 11.84, p = .002, η^2 = .28	F (1, 30) = 13.04, p = .001, η^2 = .30	n.s.	F_c (1, 30) = 7.91, p_c = .036, η^2 = .21 0 > 30	F_c (1, 30) = 9.72, p_c = .004, η^2 = .31 N < M	n.s.

600-650ms	F (1, 30) = .002, p = .96, η^2 = .001	F (1, 30) = 33.86, p < .001, η^2 = .53	F (1, 30) = 10.21, p = .003, η^2 = .25	n.s.	n.s.	F_c (1, 30) = 17.87, p_c < .001, η^2 = .43 N < M	n.s.
650-700ms	F (1, 30) = 1.38, p = .249, η^2 = .044	F (1, 30) = 31.58, p < .001, η^2 = .51	F (1, 30) = 1.37, p = .25, η^2 = .04			F_c (1, 30) = 9.72, p_c = .004, η^2 = .32 N < M	
700-750ms	F (1, 30) = 1.13, p = .297, η^2 = .04	F (1, 30) = 23.28, p < .001, η^2 = .44	F (1, 30) = .12, p = .73, η^2 = .004			F_c (1, 30) = 9.37, p_c = .020, η^2 = .24 N < M	F_c (1, 30) = 8.08, p_c = .008, η^2 = .27 N < M
750-800ms	F (1, 30) = 1.31, p = .26, η^2 = .04	F (1, 30) = 16.97, p < .001, η^2 = .36	F (1, 30) = .07, p = .79, η^2 = .002			F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 N < M	
800-850ms	F (1, 30) = 2.60, p = .12, η^2 = .08	F (1, 30) = 7.52, p = .010, η^2 = .20	F (1, 30) = .33, p = .57, η^2 = .01				
850-900ms	F (1, 30) = .04, p = .84, η^2 = .001	F (1, 30) = 4.69, p = .038, η^2 = .14	F (1, 30) = .46, p = .501, η^2 = .02				
900-950ms	F (1, 30) = .31, p = .58, η^2 = .01	F (1, 30) = 9.50, p = .004, η^2 = .24	F (1, 30) = .09, p = .77, η^2 = .003				
950-1000ms	F (1, 30) = 2.25, p = .144, η^2 = .07	F (1, 30) = .52, p = .476, η^2 = .02	F (1, 30) = .11, p = .75, η^2 = .004				

Table 5.2

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 60° from 300 to 1000ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	***Angle*** main effect (0° vs. 60°) Planar Rotation	***Stimulus Type*** main effect (normal vs. mirror) Non-planar rotation	***Rotation Angle*** × ***Stimulus Type*** interaction	**Follow-up Comparisons**			
				Angle main effect (0° vs. 60°) Planar Rotation		Stimulus Type (normal vs. mirror) Non-planar rotation	
				Normal letter	Mirror Letter	0º	60º
300-350ms	F (1, 30) = .01, p=.908, η^2= .01	F (1, 30) = 5.48, p = .026, η^2 = .15	F (1, 30) = .35, p = .56, η^2 = .01				F_c (1, 30) = 4.25, p_c = .048, η^2 = .19 N > M
350-400ms	F (1, 30)=6.25, p=.018, η^2= .17	F (1, 30) = 11.77, p = .002, η^2 = .28	F (1, 30) = .11, p = .74, η^2 = .004			F_c (1, 30) = 4.42, p_c = .044, η^2 = .20 N > M	F_c (1, 30) =15.87, p_c < .001, η^2 = .46 N > M
400-450ms	F(1,30)=13.42, p=.001,η^2 = .31	F (1, 30) = 28.03, p < .001, η^2 = .48	F (1, 30) = 2.51, p = .12, η^2 = .08		F_c (1, 30) = 12.80, p_c = .001, η^2 = .35 0 > 60	F_c (1, 30) = 7.15, p_c = .012, η^2 = .26 N > M	F_c (1, 30) =13.93, p_c = .001, η^2 = .38 N > M
450-500ms	F (1, 30)=5.15, p=.031, η^2=.15	F (1, 30) = 12.47, p = .001, η^2 = .29	F (1, 30) = 9.28, p = .005, η^2 = .24	n.s.	F_c (1, 30) = 8.08, p_c = .008, η^2 = .29 0 > 60	n.s.	n.s.
500-550ms	F (1, 30)=2.25, p=.144, η^2=.07	F (1, 30) = .06, p = .806, η^2 = .002	F (1, 30) = 17.95, p < .001, η^2 = .38	n.s.	F_c (1, 30) = 12.80, p_c = .001, η^2 = .35 0 > 60	n.s.	n.s.

550-600ms	F (1, 30) =.10, p=.750,η^2=.003	F (1, 30) = 11.84, p = .002, η^2 =.28	F (1, 30) = 13.04, p = .001, η^2 = .30	n.s.	F_c (1, 30) = 8.08, p_c = .008, η^2 = .27 0 > 60	F_c (1, 30) = 9.72, p_c = .004, η^2 = .31 N < M	n.s.
600-650ms	F (1, 30)=.12, p =.73, η^2=.004	F (1, 30) = 33.32, p < .001, η^2 = .53	F (1, 30) = 27.21, p < .001, η^2 = .48	F_c (1, 30) = 6.52, p_c = .016, η^2 = .24 0 < 60	F_c (1, 30) = 8.08, p_c = .008, η^2 = .27 0 > 60	F (1, 30) = 23.03, p < .001, η^2 = .43 N < M	n.s.
650-700ms	F (1, 30)=1.89, p =.18, η^2 =.06	F (1, 30) = 28.99, p < .001, η^2 = .49	F (1, 30) = 6.99, p = .013, η^2 = .19	F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 0 < 60	n.s.	F_c (1, 30) = 9.72, p_c = .004, η^2 = .32 N < M	n.s.
700-750ms	F (1, 30)=3.06, p =.09, η^2 = .09	F (1, 30) = 24.55, p < .001, η^2 = .45	F (1, 30) = .31, p = .58, η^2 = .01			F_c (1, 30) = 6.04, p_c = .020, η^2 = .24 N < M	F_c (1, 30) = 8.08, p_c = .008, η^2 = .28 N < M
750-800ms	F (1, 30)=3.67, p =.065, η^2=.11	F (1, 30) = 18.14, p < .001, η^2 = .38	F (1, 30) = .09, p = .76, η^2 = .003			F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 N < M	F_c (1, 30) = 5.33, p_c = .028, η^2 = .22 N < M
800-850ms	F (1, 30)=1.97, p =.17, η^2 =.06	F (1, 30) = 12.14, p = .002, η^2 = .29	F (1, 30) = .20, p = .66, η^2 = .01				F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 N < M
850-900ms	F (1, 30)=2.07, p =.16, η^2 = .06	F (1, 30) = 10.06, p = .003, η^2 = .25	F (1, 30) = .08, p = .78, η^2 = .003				
900-950ms	F (1, 30) = .42, p = .52, η^2 =.01	F (1, 30) = 11.09, p = .002, η^2 = .27	F (1, 30) = .54, p = .47, η^2 = .02				
950-1000ms	F (1, 30)=2.38, p =.13, η^2 =.07	F (1, 30) = 1.91, p = .18, η^2 = .06	F (1, 30) = .56, p = .46, η^2 = .02				

Table 5.3

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 90° from 300 to 1000ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	***Angle*** main effect (0° vs. 90°) Planar Rotation	***Stimulus Type*** main effect (normal vs. mirror) Non-planar rotation	***Rotation Angle*** × ***Stimulus Type*** interaction	**Follow-up Comparisons**			
				Angle main effect (0° vs. 90°) Planar Rotation		Stimulus Type (normal vs. mirror) Non-planar rotation	
				Normal letter	Mirror Letter	0º	90º
300-350ms	F (1, 30)=5.27, p =.029, η^2 =.15	F (1, 30) =.04, p=.850, η^2=.001	F (1, 30) = 5.25, p = .029, η^2= .15	F_c (1, 30) =4.25., p_c =.048, η^2 =.19 0 > 90	n.s.	n.s.	n.s.
350-400ms	F (1, 30) = 9.62, p = .004, η^2= .24	F (1, 30) = 6.17, p =.015, η^2 = .18	F (1, 30) = 3.13, p = .09, η^2 = .10	F_c (1, 30) =15.87, p_c < .001, η^2=.39 0 > 90		F_c (1, 30) = 4.42, p_c = .044, η^2 = .20 N > M	
400-450ms	F (1, 30)=36.63, p< .001, η^2 =.55	F (1, 30)=18.24, p <.001, η^2 =.38	F (1, 30) = .29, p = .592, η^2= .01	F_c (1, 30) =15.87, p_c < .001, η^2 = .39 0 > 90		F_c (1, 30) =7.15, p_c = .012, η^2 = .26 N > M	F_c (1, 30) = 4.25, p_c = .048, η^2=.19 N > M
450-500ms	F (1, 30)=33.64, p < .001, η^2= .53	F (1, 30)=17.44, p< .001, η^2 =.37	F (1, 30) = 6.64, p = .015, η^2= .18	F_c (1, 30) = 4.61, p_c = .040, η^2 = .20 0 > 90	F_c (1, 30) =20.27, p_c <.001, η^2 = .55 0 > 90	n.s.	F_c (1, 30) =17.87, p_c < .001,η^2 =.43 N > M
500-550ms	F (1, 30)=13.64, p= .001,η^2 = .31	F (1, 30) =3.63, p = .066, η^2= .11	F (1, 30)=33.12, p< .001, η^2 = .53	n.s.	F_c (1, 30) =20.27, p_c <.001, η^2 = .59 0 > 90	n.s.	F_c (1, 30) =12.03, p_c = .002, η^2= .46 N > M
550-600ms	F (1, 30) = .88, p = .355, η^2= .03	F (1, 30) =3.64, p = .066, η^2= .11	F (1, 30)=32.45, p < .001, η^2= .52	n.s.	F_c (1, 30) =13.93, p_c = .001, η^2 = .37	F_c (1, 30) = 9.72, p_c = .004, η^2 = .31	n.s.

					0 > 90	N < M	
600-650ms	F (1, 30) =.84, p = .367, η^2= .03	F (1, 30)=28.70, p < .001, η^2= .49	F (1, 30)=26.18, p < .001, η^2 =.47	F_c (1, 30) = 8.08, p_c = .008, η^2 = .29 0 < 90	n.s.	F_c (1, 30) =17.87, p_c < .001, η^2 = .43 N < M	n.s.
650-700ms	F (1, 30) = 5.55, p = .025, η^2= .16	F (1, 30)=26.76, p < .001, η^2= .47	F (1, 30) = 6.94, p = .013, η^2= .19	F_c (1, 30) = 9.72, p_c = .004, η^2 = .30 0 < 90	n.s.	F_c (1, 30) = 9.72, p_c = .004, η^2 = .32 N < M	n.s.
700-750ms	F (1, 30)=13.87, p =.011, η^2 =.32	F (1, 30)=13.84, p = .001, η^2= .32	F (1, 30) = 2.71, p = .110, η^2= .08	F_c (1, 30) =12.80, p_c = .001, η^2 = .35 0 < 90		F_c (1, 30) = 6.04, p_c = .020, η^2 = .24 N < M	
750-800ms	F (1, 30)=14.86, p = .001, η^2= .33	F (1, 30)=17.24, p < .001, η^2= .37	F (1, 30) = .84, p = .37, η^2 = .03	F_c (1, 30) = 9.72, p_c = .004, η^2 = .30 0 < 90		F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 N < M	
800-850ms	F (1, 30)=12.34, p = .001, η^2= .29	F (1, 30)=11.64, p = .002, η^2= .28	F (1, 30) = .06, p =.814, η^2=.002	F_c (1, 30) = 5.33, p_c = .028, η^2 = .22 0 < 90	F_c (1, 30) = 5.65, p_c = .024, η^2 = .22 0 < 90		
850-900ms	F (1, 30)=10.12, p= .003, η^2 = .25	F (1, 30) = 7.45, p = .010, η^2= .20	F (1, 30) = .18, p =.673, η^2=.006	F_c (1, 30) = 4.42, p_c = .044, η^2 = .20 0 < 90	F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 0 < 90		
900-950ms	F (1, 30) = 8.08, p = .008, η^2= .21	F (1, 30) = 9.67, p = .004, η^2= .24	F (1, 30) = .17, p =.684, η^2=.006	F_c (1, 30) = 4.09, p_c = .052, η^2 = .19 0 < 90			
950-1000ms	F (1, 30) = 4.94, p = .034, η^2= .14	F (1, 30) = 3.38, p = .076, η^2= .10	F (1, 30) = 1.46, p =.236, η^2=.047				

Table 5.4.

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 120° from 300 to 1000ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	***Angle*** main effect (0° vs. 120°) Planar Rotation	***Stimulus Type*** main effect (normal vs. mirror) Non-planar rotation	***Rotation Angle*** × ***Stimulus Type*** interaction	**Follow-up Comparisons**			
				Angle main effect (0° vs. 120°) Planar Rotation		Stimulus Type (normal vs. mirror) Non-planar rotation	
				Normal letter	Mirror Letter	0º	120º
300-350ms	F (1, 30)=2.14, p =.154, η^2=.07	F (1, 30) = .06, p =.807, η^2=.002	F (1, 30)=15.06, p = .001, η^2= .33	F_c (1, 30) = 9.72, p_c = .004, η^2 = .32 0 > 120	n.s.	n.s.	n.s.
350-400ms	F (1, 30)=23.15, p <.001, η^2 = .44	F (1, 30) = 2.26, p = .14, η^2 = .07	F (1, 30) = 9.80, p= .004, η^2 = .25	F_c (1, 30) =20.27, p_c <.001, η^2 = .54 0 > 120	n.s.	F_c (1, 30) =4.42, p_c =.044, η^2=.20 N > M	n.s.
400-450ms	F (1, 30)=48.44, p <.001, η^2 = .62	F (1, 30) = 7.40, p = .011, η^2= .20	F (1, 30) = 8.29, p = .007, η^2= .22	F_c (1, 30) =20.27, p_c <.001, η^2 = .62 0 > 120	F_c (1, 30)=13.93, p_c = .001, η^2 = .37 0 > 120	F_c (1, 30) =7.15, p_c =.012, η^2=.26 N > M	n.s.
450-500ms	F (1, 30)=67.78, p < .001, η^2= .69	F (1, 30) = 4.31, p = .046, η^2= .12	F (1, 30) = .001, p =.980, η^2=.001	F_c (1, 30) =20.27, p_c <.001, η^2 = .58 0 > 120	F_c (1, 30) =20.27, p_c <.001, η^2 = .55 0 > 120		
500-550ms	F (1, 30)=29.97, p < .001, η^2= .50	F (1, 30) =.10, p= .755,η^2= .003	F (1, 30)=11.35, p = .002, η^2= .27	n.s.	F_c (1, 30) =20.27, p_c <.001, η^2 = .63 0 > 120	n.s.	n.s.
550-600ms	F (1, 30) = 5.82, p = .022, η^2= .16	F (1, 30) = 5.92, p = .021, η^2= .17	F (1, 30)=26.13, p < .001, η^2= .47	n.s.	F_c (1, 30) =20.27, p_c <.001, η^2 = .55 0 > 120	F_c (1, 30) =9.72, p_c =.004, η^2=.31 N < M	F_c (1, 30) = 4.61, p_c = .040, η^2 = .20 N > M

600-650ms	F (1, 30) = .24, p = .63, η^2= .008	F (1, 30)=17.61, p < .001, η^2= .37	F (1, 30)=60.34, p < .001, η^2= .67	F_c (1, 30) = 5.65, p_c = .024, η^2 = .22 0 < 120	F_c (1, 30) =17.87, p_c < .001, η^2 = .43 0 > 120	F_c(1, 30)=17.87, p_c <.001, η^2=.43 N < M	F_c (1, 30) = 15.87, p_c < .001, η^2 = .39 N > M
650-700ms	F (1, 30) = 4.57, p = .041, η^2= .13	F (1, 30)=20.31, p< .001, η^2 = .40	F (1, 30)=20.97, p < .001, η^2= .41	F_c (1, 30) =12.03, p_c = .002, η^2 = .35 0 < 120	n.s.	F_c (1, 30) =9.72, p_c =.004, η^2=.32 N < M	n.s.
700-750ms	F (1, 30)=19.81, p< .001, η^2 = .40	F (1, 30)=15.92, p < .001, η^2= .35	F (1, 30) = 6.81, p = .014, η^2= .19	F_c (1, 30) =20.27, p_c < .001, η^2 = .45 0 < 120	n.s.	F_c (1, 30) =6.04, p_c =.020, η^2=.24 N < M	n.s.
750-800ms	F (1,30) =17.06, p < .001, η^2= .36	F (1, 30)=10.38, p = .003, η^2= .26	F (1, 30) = 4.29, p = .047, η^2= .13	F_c (1, 30) =13.93, p_c = .001, η^2 = .37 0 < 120	n.s.	F_c (1, 30) =4.09, p_c =.052, η^2=.19 N < M	n.s.
800-850ms	F (1, 30)=22.66, p < .001, η^2= .43	F (1, 30) =7.87, p = .009, η^2= .21	F (1, 30) = .74, p = .397, η^2= .02	F_c (1, 30) =12.03, p_c = .002, η^2 = .35 0 < 120	F_c (1, 30) = 9.72, p_c = .004, η^2 = .33 0 < 120		
850-900ms	F (1, 30)=16.02, p < .001, η^2= .35	F (1, 30) = 5.78, p = .023, η^2= .16	F (1, 30) = .16, p =.691, η^2=.005	F_c (1, 30) = 9.72, p_c = .004, η^2 = .21 0 < 120	F_c (1, 30) = 7.15, p_c = .012, η^2 = .25 0 < 120		
900-950ms	F (1, 30)=12.66, p = .001, η^2= .30	F (1, 30) = 13.18, p = .001, η^2 = .31	F (1, 30)= .09, p = .769, η^2= .30	F_c (1, 30) = 6.04, p_c = .020, η^2 = .23 0 < 120	F_c (1, 30) = 6.52, p_c = .016, η^2 = .24 0 < 120		
950-1000ms	F (1, 30) = 5.69, p = .024, η^2= .16	F (1, 30)=2.64, p =.114, η^2=.08	F (1, 30) = 2.54, p = .122, η^2= .08		F_c (1, 30) = 5.33, p_c = .028, η^2 = .22 0 < 120		F_c (1, 30) = 4.82, p_c = .036, η^2 = .21 N < M

Table 5.5

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 150° from 300 to 1000ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	***Angle*** main effect (0° vs. 150°) Planar Rotation	***Stimulus Type*** main effect (normal vs. mirror) Non-planar rotation	***Rotation Angle*** × ***Stimulus Type*** interaction	**Follow-up Comparisons**			
				Angle main effect (0° vs. 150°) Planar Rotation		Stimulus Type (normal vs. mirror) Non-planar rotation	
				Normal letter	Mirror Letter	0º	150º
300-350ms	F (1, 30)=3.87, p =.058, η^2=.11	F (1, 30) = .164, p = .69, η^2 = .005	F (1, 30) = 3.86, p = .059, η^2= .11	F_c (1, 30)=4.09, p_c =.052, η^2=.19 0 > 150			
350-400ms	F(1, 30)=37.49, p< .001, η^2=.56	F (1, 30) = 4.97, p = .033, η^2 = .14	F (1, 30) = 4.55, p = .041, η^2= .13	F_c(1, 30)=20.27, p_c<.001, η^2= .57 0 > 150	F_c (1, 30) = 8.08, p_c = .008, η^2 = .28 0 > 150	F_c (1, 30) =4.42, p_c =.044, η^2=.20 N > M	n.s.
400-450ms	F(1, 30)=45.92, p <.001, η^2=.61	F (1, 30) = 5.74, p = .023, η^2 = .16	F (1, 30) = 8.29, p = .007, η^2= .22	F_c(1, 30)=20.27, p_c <.001, η^2=.61 0 > 150	F_c (1, 30) =16.80, p_c <.001, η^2 = .41 0 > 150	F_c (1, 30) =7.15, p_c =.012, η^2=.26 N > M	n.s.
450-500ms	F(1, 30)=62.51, p <.001, η^2=.68	F (1, 30) = 1.43, p = .24, η^2 = .05	F (1, 30) = .98, p = .33, η^2 = .03	F_c(1, 30)=20.27, p_c<.001, η^2= .63 0 > 150	F_c (1, 30) =20.27, p_c <.001, η^2 = .59 0 > 150		
500-550ms	F(1, 30)=65.90, p<.001, η^2= .69	F (1, 30) = 4.19, p = .049, η^2 = .12	F (1, 30) = 1.93, p = .175, η^2= .06	F_c(1, 30)=20.27, p_c<.001,η^2=.511 0 > 150	F_c (1, 30) =20.27, p_c <.001, η^2 = .53 0 > 150		
550-600ms	F(1, 30)=34.11, p <.001, η^2=.53	F (1, 30) = 8.01, p = .008, η^2 = .21	F (1, 30)=16.34, p < .001, η^2= .35	n.s.	F_c (1, 30) =20.27, p_c <.001, η^2 = .71 0 > 150	F_c (1, 30) =9.72, p_c =.004, η^2=.31 N < M	n.s.

600-650ms	F (1, 30) =6.27, p =.018, η^2=.17	F (1, 30) = 9.98, p = .004, η^2 = .25	F (1, 30)=50.02, p < .001, η^2= .63	n.s.	F_c (1, 30) =20.27, p_c <.001, η^2 = .61 0 > 150	F (1, 30) = 23.03, p < .001, η^2 = .43 N < M	n.s.
650-700ms	F (1, 30) = .23, p = .63, η^2= .01	F (1, 30)=3.87, p=.058, η^2=.11	F (1, 30)=35.28, p < .001, η^2= .54	F_c (1, 30) =5.06, p_c =.032, η^2=.22 0 < 150	n.s.	F_c (1, 30) =9.72, p_c =.004, η^2=.32 N < M	n.s.
700-750ms	F (1, 30) =9.97, p =.004, η^2=.25	F (1, 30) = .51, p =.48, η^2= .02	F (1, 30)=30.96, p < .001, η^2= .51	F_c(1, 30)=20.27, p_c <.001, η^2=.45 0 < 150	n.s.	F_c (1, 30) =6.04, p_c =.020, η^2=.24 N < M	F_c (1, 30) = 12.03, p_c = .002, η^2 = .34 N > M
750-800ms	F(1, 30)=10.27, p =.003, η^2=.26	F (1, 30) = .81, p=.375,η^2=.03	F (1, 30)=15.81, p < .001, η^2= .35	F_c(1, 30)=13.93, p_c=.001, η^2= .38 0 < 150	n.s.	F_c (1, 30) =4.09, p_c =.052, η^2=.19 N < M	n.s.
800-850ms	F(1, 30)=19.64, p<.001, η^2= .40	F (1, 30) = .03, p=.863, η^2=.001	F (1, 30)=15.66, p < .001, η^2= .34	F_c(1, 30)=13.93, p_c=.001, η^2= .49 0 < 150	n.s.	n.s.	F_c (1, 30) = 7.15, p_c = .012, η^2 = .25 N > M
850-900ms	F(1, 30)=42.68, p <.001, η^2=.59	F (1, 30)=1.34, p=.256, η^2=.04	F (1, 30) = 4.53, p = .042, η^2= .13	F_c(1, 30)=20.27, p_c<.001, η^2= .57 0 < 150	F_c (1, 30) =13.93, p_c =.001, η^2 = .38 0 < 150	n.s.	n.s.
900-950ms	F(1, 30)=56.48, p <.001, η^2=.65	F (1, 30) =.40, p =.53, η^2= .01	F (1, 30)=13.33, p = .001, η^2= .31	F_c(1, 30)=20.27, p_c <.001, η^2=.70 0 < 150	F_c (1, 30) =11.47, p_c =.002, η^2 = .34 0 < 150	n.s.	n.s.
950-1000ms	F(1, 30)=30.23, p <.001, η^2=.50	F (1, 30) = .13, p=.72, η^2=.004	F (1, 30) = .50, p = .487, η^2= .02	F_c(1, 30)=20.27, p_c<.001, η^2= .44 0 < 150	F_c (1, 30) = 8.08, p_c = .008, η^2 =.27 0 < 150		